THE FORAGING BEHAVIOUR OF GRANIVOROUS BIRDS: A MECHANISTIC PERSPECTIVE

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Abstract

1. The functional response, i.e. the feeding rate as a function of prey density, links resource availability to population level demographic rates. The functional response is often central to behavioural-based population models that predict the effect of environmental changes on populations based on the assumption that each individual tries to maximise its fitness at all times.

2. The functional response is a well studied phenomenon for some groups of foragers and many mechanistic models of the functional response have been derived to account for variations in foraging behaviour. However, only a few functional response models have been applied to granivorous farmland birds and these models often have simplifying assumptions that are likely to be inappropriate for these foragers. Consequently, the functional response models that often lie at the core of behavioural-based population models are untested and quite possibly provide a poor prediction of the functional response.

3. The objectives of this thesis are to: (i) test the ability of functional response models to predict the functional response of granivorous birds; (ii) identify incorrect assumptions in these models; and (iii) derive new functional response models that better describe the observed behaviour of these foragers.

4. Here I have found that many of the underlying assumptions of simple functional response models are inappropriate for granivorous birds and several new mechanistic models have been derived that attempt to describe the behaviour more accurately. Vigilance was shown to frequently interact with

incompatible behavioural processes (i.e. searching) and affect the feeding rate at low prey densities. Handling time was divided into two components (i.e. attack and process) and a simple mechanistic model was derived to predict the attack component of prey handling. The searching mode of granivorous birds was shown to be akin to a pause-travel forager at low prey densities and, lastly, habitat structure was shown to reduce the feeding rate by restricting the searching area.

5. These finding will help in the development of more biologically 'realistic' functional response models and provide a more accurate prediction of the functional response when used to predict the effect of environmental change on the intake rate of foragers.

Contents

List of Figures

List of Tables

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Declaration

I confirm that the work presented in this thesis is my own, with the following exceptions:

Chapter 2 is published in collaboration with Richard Stillman and James Bullock as

> Baker, D.J., Stillman, R.A. & Bullock, J.M. (2009) The effect of habitat complexity on the functional response of a seed-eating passerine. Ibis, 151, 547-558.

Chapter 3 is published in collaboration with Richard Stillman, Barbara Smith, James Bullock and Ken Norris as

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Chapter 4 is published in collaboration with Richard Stillman, Simon Smart, James Bullock and Ken Norris as

> Baker, D.J., Stillman, R.A., Smart, S.M., Bullock, J.M. & Norris, K.J. (In press) Are the costs of routine vigilance avoided by granivorous foragers? Functional Ecology.

Simon Smart collected the raw functional response data for the yellowhammer, tree sparrow and linnet analysis. The functional response models in chapters 3 and 5 were derived in collaborated with Richard Stillman.

David J. Baker

Chapter 1

Introduction

1.1 The functional response

> "Firstly, there must be a functional response to an increase in the host density, because of the increased availability of victims: as host density rises, each enemy will attack more host individuals, or it will attack a fixed number more rapidly"
>
> Solomon (1949)

The functional response, defined as the intake rate of a forager as a function of prey density (Holling 1966), has been an important concept in ecology and has received much attention since Solomon (1949), and later Holling (1959b), first published their influential papers. It was the former paper that coined the term 'functional response' and the latter paper that introduced the first mechanistic model for describing the functional response of a predator. Much of the importance of the functional response lies in the link it provides between trophic levels within an ecosystem (Gentleman & Neuheimer 2008) and in the insight it has provided into the dynamics of predator-prey systems (Oaten & Murdoch 1975; Nilsson 2001; Rudolf 2008). Functional responses can broadly be split into three

types, although several additional variations have been proposed (i.e. type IV (Holling 1959b)).

1.1.1 Type I functional response

Type I functional responses (Fig. 1.1a) are characterised by a linear increase in feeding rate with increasing prey density up to a threshold level above which the feeding rate remains constant (Jeschke, Kopp & Tollrian 2004). For a forager to exhibit a type I functional response it must have negligible handling and digestion time so that prey is consumed at the rate of encounter, until a maximum feeding rate is reached. Such functional responses are almost exclusively restricted to filter feeders, where the intake rate is simply dependent on the quantity of food passing through the filter systems during any time interval (Jeschke *et al.* 2004).

1.1.2 Type II functional response

Type II functional responses (Fig. 1.1b) are characterised by a feeding rate that increases at a decelerating rate with prey density, eventually reaching a threshold feeding rate at high prey densities (Holling 1959b). The type II functional response is found commonly and across a broad range of taxa, including both invertebrates (Holling 1966; Hassell *et al.* 1976), and vertebrates (grazing/browsing herbivores (Gross *et al.* 1993); pause-travel predators (Goss-Custard *et al.* 2006; Poole *et al.* 2007); mammalian predators (Nilsen *et al.* 2009)). The maximum feeding rate might be limited by the ability to handle individual prey items or by digestive constrains, such as stomach capacity and digestion rate (Jeschke *et al.* 2002). The type II functional response will be the main focus of this thesis.

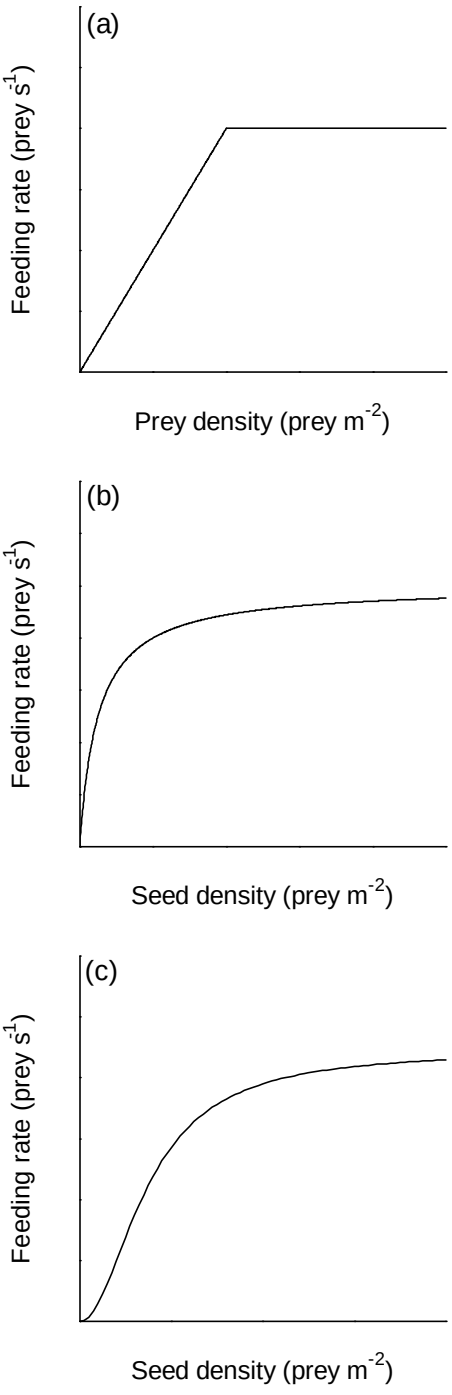

Figure 1.1: Three types of functional response as defined by Holling's (1959b): (a) Type I functional response; (b) Type II functional response; and (c) Type III functional response.

1.1.3 Type III functional response

Type III functional responses (Fig. 1.1c) are sigmoidal in shape characterising an initially slow increase in feeding rate at low prey density followed by an acceleration in the rate at which feeding rate increases with higher prey densities; the feeding rate slows again at high densities as it approaches its asymptote. The type III functional response has been attributed to several different mechanisms, including a learning function (Real 1979) where the predator becomes more alert to a prey as their density increases (i.e. search image (Morgan & Brown 1996)). Alternative explanations include, increasing detectability of prey with density, which could result from the availability of protective shelter, and prey switching (Murdoch 1973). However, addressing the latter Asseburg (2006) showed that prey switching is not necessarily a property of type III functional responses and can occur in type I and II responses.

Type III functional responses have been identified in many different foragers from a diverse taxonomic range (Kempf, Floeter & Temming 2008; Sarnelle & Wilson 2008) and are probably very common when prey switching, prey cryptticity and fluctuating abundances of different prey are taken into account (Getty 1985; Morozov 2010).

1.2 Mechanistic models of the functional response

Mechanistic descriptions of foraging behaviour have deep roots in ecology beginning with Holling's (1959b) attempt to describe the functional response of a human 'predator' and since this time mechanistic models have been derived for a diverse range of foragers and scenarios (Hollings 1966; Stephens & Krebs 1986; Jeschke *et al.* 2002). It is noted by Holling (1966) that the earliest models

of predator-prey interactions (i.e. Lotka-Volterra equation) use the language of 'classical physics', presenting the models as differential equations. In an attempt to understand the underlying mechanisms that leads to the observed patterns of predator-prey interactions Holling, and later others (see Jeschke *et al.* (2002) for a thorough review), began to formulate simple models that tried to represent the observed processes of predation. The aim here was to put the need for biological realism foremost, at the expense of mathematical precision, and to explore the mechanistic processes of predation; once these mechanisms were understood more 'precise mathematical' models could be derived to describe the same processes (Holling 1966).

Holling's early approach was based on the notion that complex processes could be understood by studying the 'action and interaction of a number of discrete components' (Holling 1966). This was termed an 'experimental component analysis' (Holling 1963) and is succinctly described by the following quote:

> "The crux of the proposed approach lies in the belief that every process, however complex, can be fragmented into its constituent parts"
>
> Holling (1963)

The mechanistic term is used to distinguish these models from phenomenological models, that are based on empirically determined relationship between populations and their environment without attempting to describe an underlying mechanism (Stephens *et al.* 2003, Sutherland 2006). Understanding behaviour from the properties and interactions of the underlying processes differs sharply from these pattern-orientated modelling approaches that make no *a priori* assumptions towards the underlying processes that give rise to a behaviour (Norris 2004). However, it is difficult to truly define the term mechanistic and to provide a clear

demarcation between mechanistic and non-mechanistic models as every process used to describe a behaviour can itself be described in mechanistic terms (Bolker 2008). Nevertheless, to avoid *reductio ad absurdum* a functional definition is required and it must be accepted that any model described as 'mechanistic' will have some phenomenological components (Stephens *et al.* 2003; Sutherland 2006; Bolker 2008). Throughout this thesis any mathematical model that explicitly attempts to describe a behaviour through the interactions of 'meaningful' (Bolker 2008) and measurable component processes will be termed mechanistic (Cox *et al.* 2006), however, the properties, assumptions and limitations of the models will be clearly discussed providing clarity beyond simplistic definitions.

Describing a behaviour mechanistically requires a thorough understanding of the behavioural patterns and processes, including how these processes interact with one another and how they are affected by external variables, i.e. prey density or interference competition. Holling (1963) described an experimental approach to understanding 'population processes' and used this approach to explore predation in a series of seminal papers (Holling 1959a, 1959b, 1965, 1966). The stages of such an analysis involve the identification of the basic components of the process and the development of preliminary hypotheses as to the actions and interactions of the components based on experimental evidence. Mathematical expressions for the process can then be derived that included the basic components of the process, which are then built upon to form more complex models as new experimental evidence becomes available. It is the experimental analysis of the component processes that is key to the derivation of biologically plausible functional response models and this careful approach is evident in Holling's publications (Holling 1963, 1965, 1966).

1.2.1 The Holling's disc model

The Holling's disc model (Holling 1959b) (equation 3.3.4) describes the shape of a type II functional response in terms of an interaction between searching for a prey item and subsequently handling each item. The searching rate is a function of prey density and thus as prey become more abundant they are encountered with increasing frequency. As the encounter rate increases the time spent searching becomes a smaller proportion of the foraging time and the handling time begins to limit the feeding rate. As the feeding rate approaches the asymptote the time spent searching tends to zero and the feeding rate is set by the time taken to handle each prey. The Holling's disc equation is given by

$$F = \frac{aD}{1+aDH} \tag{1}$$

where F = feeding rate, a = searching rate, D = prey density and H = handling time. This model has several key assumptions:

- prey is of a single type and randomly distributed
- prey handling and searching are the only significant behavioural states
- prey handling and searching are mutually exclusive behavioural states
- handling time and searching rate are invariant with prey density
- predators are handling limited at high densities

Holling (1959b) described this model as a 'basic functional response' that included only the components of foraging that must be present in all situations. Whilst this model might contain the minimum number of behavioural components their interactions are constrained by the assumptions and, therefore, whether

this is the basic model for all foragers is questionable. For example, many species can search whilst handling and therefore the assumption of mutually exclusive handling and searching is incorrect for these species (Fortin *et al.* 2004b; Smart *et al.* 2008). However, this model is often considered as the null mechanistic functional response model and has provided a starting point for the derivation of increasingly realistic models, including those tailored to specific foragers and foraging models (see section 1.2.2).

1.2.2 Further developments and unanswered questions

Whilst this simple model has played a central role in foraging theory over the past 50 years contemporary publications were attempting to incorporate increasingly realistic mechanisms into foraging models (Holling 1966) to account for the behavioural processes observed in real predator-prey interactions. These have tended to follow several themes, although the popularity of each theme and the degree to which they have been explored varies considerably. For instance, multiple prey functional response models have been the focus of much research (i.e. Murdoch 1973; Gentleman *et al.* 2003), however, predator vigilance has only very recently received attention (Fortin *et al.* 2004a, 2004b; Smart *et al.* 2008). This might be due to the common use of invertebrate predator-prey systems to test functional response models, where behaviours such as vigilance are more difficult to observe than in vertebrate systems.

There are many known phenomenon that violate the assumptions of commonly used functional response models and whilst some have been addressed in new models others still remain unresolved. In this section I will discuss the developments in functional response models and the areas that are still to be fully explored.

1.2.2.1 Prey depletion

The Steady State Satiation Model of Jeschke & Hohberg (2008) allowed for the depletion of prey during a foraging experiment and this has long been noted as a potential confounding factor in functional response experiments (Royama 1971; Rogers 1972), especially when the forager searches randomly for prey. The first model to account for the number of prey eaten was the Rogers (1972) random-predator model (Equation 1.2.2.1):

$$N_{eat} = N\left(1 - e^{-a(T_t - N_{at} \times b)}\right) \tag{2}$$

where N_{eat}= number of prey eaten, a = attack coefficient, b = handling time, T_t= total foraging time and N_{at}= number of prey attacked. These models are used often in invertebrate functional response experiments where the predator is randomly searching for the prey and prey are able to move constantly (i.e. Collins, Ward & Dixon 1981). Where the prey are immobile and the predator searches systematically the effect of depletion in a functional response experiment can be avoided if measurement are only made in 'new' patches where no previous foraging has occurred.

1.2.2.2 Hunger, satiation and digestion

Forager hunger/satiation was understood to be an important component of foraging behaviour that could have a significant effect on the feeding rate by influencing the motivation to forage (Rashevsky 1959; Holling 1966; Jeschke *et al.* 2002). Holling's (1966) detailed study on the effect of hunger on the feeding behaviour of mantids showed that hunger can affect the attack distance and the motivation to attack, yet has no effect on prey handling and attack speed. Jeschke

et al. (2002) derived a model that accounts for the reduced motivation to forage by assuming a steady state of hunger at a given prey density (equilibrium of ingestion and digestion); this model is termed the Steady-State Satiation (SSS) model. This model was extended (Jeschke & Hohberg 2008) to allow variations in hunger with ingestion and digestion, and shown to give the best prediction of the observed functional response in a tardigrade-nematode system (compared with the SSS and Holling's disc models).

Predator satiation will often limit the feeding rate of predators over the long-term, but for many foragers prey handling limits the feeding rate over the course of a single foraging bout, i.e. their instantaneous intake rate is handling limited. For example, Smart *et al.* (2008) showed that the functional response of corn buntings *Miliara calandra* L measured over the course of a single feeding bout could be predicted using a functional response model that assumes the forager is handling limited. However, such species retreat to cover to reduce their predation risk (Whittingham & Evans 2004) and, therefore, are unlikely to be seen to be digestion-limited when feeding in the open. Conversely, shorebirds remain on the feeding patch even when satiated and, therefore, their functional responses are not predicted by handling-limited functional response models (Goss-Custard *et al.* 2006).

1.2.2.3 Overlapping behavioural states

The assumption that searching and handling are non-overlapping foraging modes is not appropriate for many foragers and several models have been derived that accommodate such an interaction (Spalinger & Hobbs 1992; Smart *et al.* 2008). For example, many herbivores can search for the next bite whilst still chewing the previous bite (Spalinger *et al.* 1992) and there is even potential to crop more

bites before finishing handling the previous one (Fortin *et al.* 2004a). Smart *et al.* (2008) derived several models that allowed handling, searching and anti-predator vigilance to overlap, but found these models could not predict the observed functional response using experimentally measured behavioural parameters better than the Holling's disc model. Fortin *et al.* (2004a) allowed handling to overlap with searching and interference from other foragers and showed that 'multi-tasking' can buffer the feeding rate from potentially costly behaviours, such as vigilance and interference competition. Where handling and searching overlap functional response models that omit this behavioural interaction will underestimate the feeding rate and possibly predict time-constraints on foraging where none exist.

1.2.2.4 Adaptive behaviour

Adaptive behaviour, such as increasing the rate of searching or decreasing the time spent handling as prey become more abundant, has been observed (Thompson 1975; Hassell *et al.* 1977; Smart *et al.* 2008) and might even be common place (Abrams 1990). Such adaptations can have a significant effect on the functional response, greatly affecting the predictions of model where these characteristics are included (Smart *et al.* 2008). Abrams (1990) commented that 'if such adaptive variation is the rule rather the exception, it argues against indiscriminate fitting of data using the fixed-parameter disc equation'. However, despite considerable exploration of the effect of prey density on searching and handling behaviour (Stephens & Krebs 1986; Jeschke *et al.* 2002) the development of functional response models that incorporate such adaptive behaviour has not progressed far.

Much of the difficulty lies in a lack of a mechanistic handling time model

that can account for the changes in handling induced by changes in the foraging conditions. For example, the marginal value theorem predicts that patch residency will be related to the rate of gain experienced in the current patch and the time taken to move to a more profitable patch (Charnov 1976; Stephens & Krebs 1986). Considering a single prey item as a patch, prey handling times have been shown to relate to prey density, and therefore the time taken to catch another prey, with individual prey items exploited to a lesser extent when prey are abundant (Cooper & Anderson 2006; Hohberg & Traunspurger 2009). Additionally, prey handling times can be affected by interference competition (Johnson *et al.* 2001), especially when kleptoparasitism is common place, as shorter handling times reduce opportunities for food stealing (Stillman *et al.* 2002). Such adaptive handling behaviours must be understood from a mechanistic perspective before their effects can be accounted for in a mechanistic model.

Prey density affects the prey encounter rate and given a constant searching rate this is often assumed to be linearly related to prey density. However, several recent studies have shown that even with a constant searching rate the prey encounter rate can increase non-linearly with prey density because predators detect and target the most conspicuous prey items first and these are encountered at a higher rate than less conspicuous prey (Mols *et al.* 2004; Ioannou *et al.* 2008). Gendron & Staddon (1983) developed a functional response model in which the probability of detecting prey was inversely related to the searching rate and crypticity of the prey. The model was used to explore the optimal searching rate given two prey with different levels of crypticity and different relative abundances, therefore allowing searching rate to vary with the foraging conditions.

1.2.2.5 Learning behaviour and prey switching

Learning behaviour by a predator (Holling 1965) and prey switching (Van Leeuwen, Jansen & Bright 2007) are two common behaviours and are often invoked to explain the sigmoidal functional response exhibited by some predators (Real 1977). Hassell *et al.* (1977) found a sigmoidal functional responses in invertebrate foragers even when there was only one prey type present and hypothesised that the predator increases its searching rate as prey density increases. Akre and Johnson (1979) hypothesised that prey switching behaviour in damselfly naiads, which resulted in a type III functional response, was caused by the use of two different searching modes (ambush and walking) that affected the encounter rate with the two prey, one motile and one sessile. Many functional response experiments are conducted in simple single prey conditions that under represent the complexity experienced by wild foragers encountering multiple prey types. Search image has been shown to influence prey choice (Morgan & Brown 1996) and adaptation to an abundant novel prey can occur slowly; however, once this adaptation has occurred there will be an effect on feeding rate relative to the density of this novel prey.

Several multi-prey functional response models have been derived and used to explore optimal diet choices and the effect of relative abundance and conspicuousness on the functional response (Murdoch & Oaten 1973; Gendron & Staddon 1983; Gentleman *et al.* 2003; Asseburg 2006). Gendron & Staddon (1983) have shown that the optimum search rate is a trade-off between prey detection and the frequency of encounter. The optimum search rate will depend on the conspicuousness of the target prey and their abundance. When multiple prey types are present an abundant but cryptic prey might be excluded from the diet in preference for a conspicuous prey. The degree to which this affects wild animals might

vary depending on the predictability of the forager's diet and conservatism in their prey choices.

Type III functional response models have been explored thoroughly (Colton 1987; Gentleman et al. 2003; Asseburg 2006) and shown to have stabilising effects on predator-prey dynamics (Oaten & Murdock 1975a, 1975b; van Baalen *et al.* 2001).

1.2.2.6 Conclusion: functional response models

From such a simple start this wide array of models have been derived to include the observed processes of some predator-prey systems and whilst this research has covered a wide range of predator-prey systems and included a broad range of processes there are still many important questions that remain to be answered. Many of these models are tailored to a particular predator-prey system with assumptions that invalidate their wider applicability; however, there is much similarity between foragers and their foraging modes that suggests the potential for a unified functional response model, or certainly models with greater flexibility and broader applicability.

1.3 Functional responses of granivorous birds: current status and key knowledge gaps

1.3.1 Target species

Granivorous foragers are those that consume the seeds of plants, including commercial crops, as their primary source of food for a significant proportion of their life cycle. Many bird species that are classified as 'granivorous' feed their young on invertebrates (Brickle & Harper 1999; Holland *et al.* 2006) during

the breeding season, however, these species are reliant on seeds for most of the non-breeding season. This thesis will focus predominantly on wintering granivorous passerines, such as those farmland specialists that remain on UK farmland throughout the winter and rely on seeds for the majority of the non-breeding season.

1.3.2 The foraging behaviour of granivorous birds from a mechanistic perspective

The foraging behaviour of most granivorous farmland birds is rather simple due to the properties of the prey (i.e. seeds), which are immobile and have few defences against avian foragers. Two main foraging modes exists: searching – characterised by a head-down posture and continuous movement (depending on the prey density); and handling – characterised by rapid movement towards the target prey and a head-up posture and bill movement while processing. These are the basic components of the functional response model (Holling 1959b), i.e. Holling's disc model, although even for a simple predator-prey system there are many behaviours and interaction not accounted for by such simple models.

1.3.3 Functional responses applied to granivorous birds

The first true test of the ability of a mechanistic functional response model to describe the observed functional response of a granivorous farmland bird species was that of Smart *et al.* (2008). Here the behavioural parameters associated with several different functional response models were measured experimentally and the model's ability to predict the functional response using these parameters tested. The Holling's disc model was shown to predict the functional response better than several more 'biologically plausible' models despite some clear vio-

lations of the model's assumptions. For example, Smart *et al.* (2008) showed that the handling time was negatively correlated with prey density yet when this variation was incorporated into the Holling's disc model a poor fit to the observed data was found.

Previously, the functional response of granivorous birds was assumed to conform to the assumptions of the Holling's disc model and the behavioural parameters were estimated by fitting this model to observed functional response data (Robinson 1997). Robinson (1997) showed that yellowhammers, corn bunting and skylark had a type II functional response but did not attempt to predict the observed functional response using measured behavioural parameters, thus the suitability of the Holling's disc models was not tested here. Similarly, Holmes (2002) derived estimates of 'searching rate' and 'handling time' by fitting the Holling's disc model to the observed functional response of chaffinches feeding on a variety of seeds. Whilst these studies appear to show a type II functional response to a single prey type in several granivorous bird species they provide little insight into the foraging mechanisms of these species and do not test the assumption of the disc model.

In general our understanding of the foraging behaviour of granivorous birds is moderately advanced, benefiting in recent years from many insightful studies. Thus, whilst our progress towards understanding the functional response of these species from a mechanistic perspective might be in its infancy there is a strong knowledge base to draw upon when deriving new models.

1.3.4 Searching behaviour

Aside from prey density (discussed in 1.2.2.4) searching behaviour is affected by the presence of vegetation, with higher vegetation reducing the detectability

of potential prey (Butler & Gillings 2004). Whittingham and Markland (2002) found that seed colour relative to the background could significantly affect the searching efficiency and, consequently, the feeding rates of canaries *Serinus canaries* L. Searching rates were lower on grass substrates than soil substrates even when more conspicuous seeds were used in the former treatment: the authors suggest that the increased surface area created by the grass substrate is the most probable cause of this decreased feeding rate. Similarly, Jones, Krebs and Whittingham (2006) show that prey crypticity affected patch choice (obstructed versus unobstructed) because searching times increase with great crypticity leading to lower vigilance levels; this is compounded when foraging in an obstructed habitat.

Measuring searching rates within functional response models is difficult as it requires knowledge of the perceptual fields of the forager and the effect of prey crypticity, habitat structure, ambient light conditions and the effect of distance on the detection function (Andersson 1981; Getty & Pulliam 1993). Getty & Pulliam (1993) showed that prey crypticity reduced the instantaneous rate of detection and that this decreased with distance. Complex detection functions have been applied to granivorous foragers (Getty & Pulliam 1991) in which prey detection is a function of distance and other factors that reduce detection. However, these remaining factors are reduced into a single parameter K that must be estimated by fitting the model to observed data, thus our understanding of the detection function gains little from such an approach. Several authors have estimated the searching rate from the maximum distance over which a bird is observed to attack a prey and the speed they travel while searching (Fortin *et al.* 2004a; Stillman & Simmons 2006). However, Poole *et al.* (2007) showed that by assuming that the search area was defined as a circle with a radius equal to the maximum

attack distance the area searched was consistently overestimated. There are no deterministic functions to-date that can account for the complexities of searching and, therefore, simplifying assumptions must be made to estimate this important functional response parameter.

1.3.5 Prey handling behaviour

Prey handling often limits the feeding rate at high prey densities and, therefore, is a most important functional response parameter. The Holling's disc model assumes handling time is invariant with prey density, however, many studies have suggested that adaptive behaviour affects this parameter (Hassell *et al.* 1977; Abrams 1990; Smart *et al.* 2008). Holling defined handling time as: (i) the time spent pursuing and subduing each prey; (ii) the time spent processing each prey; and (iii) the time spent in a digestive pause. The handling times of granivorous birds are often amalgamated into a single parameter (Robinson *et al.* 1997; Smart *et al.* 2008), however, several studies have suggested that the three stages of handling have very different properties, which can affect their interaction with other behavioural processes. For example, Cowlishaw *et al.* (2004) showed that for species that can handle prey in a head-up posture handling time could be divided into two components based on their compatibility with head-up vigilance. The initial phase of handling involves the pursuit and capture phase that is incompatible with vigilance, but the processing phase that follows, where the prey is consumed allows for overlapping handling and vigilance: this can greatly affect the impact of anti-predator vigilance on the feeding rate.

For both searching rate and handling times of granivorous birds there are considerable variations in the estimates of these parameters in the literature. For handling times this variation is in part due to variations between prey types, i.e.

seed hardness (Van Der Meij & Bout 2004), and possibly due to different levels of prey exploitation as prey availability changes (i.e. the marginal value theorem). However, much of this variation must be due to the way handling times were measured, as many studies used non-video based technique to measure handling time in the range of 1-2 second (i.e. Pulliam 1985; Keating *et al.* 1992; Hrabar & Perrin 2002) and the accuracy of these measurement should be doubted. Where video technology has been used to measure handling time the ranges show more consistency, although there is still much unaccounted variation (i.e. Van Der Meji & Bout 2005; Soobramoney & Perrin 2007).

1.3.6 Vigilance and the functional response

The new functional response models derived in Smart *et al.* (2008) include several that incorporate anti-predator vigilance and also allow searching, handling and vigilance to interact in distinct ways; these were tested alongside the Holling's disc model (see Fig. 1.2). The Holling's disc model assumes that searching and handling are mutually exclusive behavioural states, a questionable assumption for any foragers, yet the models that allowed these components to overlap produced a poor fit to the observed data. Similarly, anti-predator vigilance had no effect on the functional response model when allowed to overlap with handling, producing an identically fit to the observed data as the Holling's disc model parameterised using the same behaviour measurements. This is because the proportion of time spent vigilant was always less than the handling time and, therefore, vigilance could always be accomplished during handling where it incurs little or no cost (Cowlishaw *et al.* 2004). Whether anti-predator vigilance is necessary for such species is unknown and requires a more thorough exploration of the patterns of vigilance and how vigilance interacts with other foraging

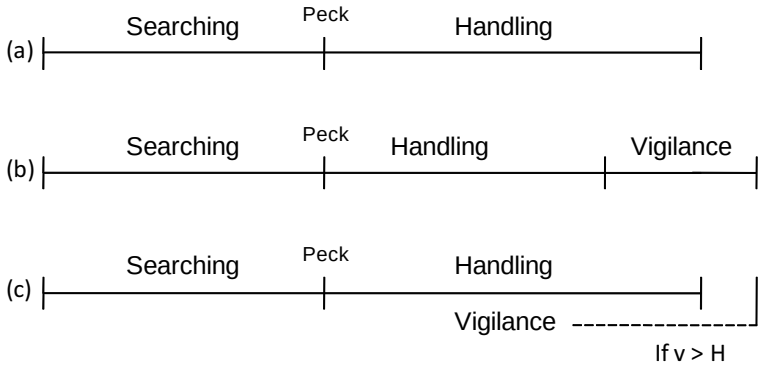

Figure 1.2: A diagramatic representation of the foraging states and their interactions as assumed by the (a) the Holling's disk model, (b) model 2 and (c) model 4, both from Smart et al (2008). v = the proportion of time spent vigilant and H = the handling time.

behaviours.

Several studies have shown the importance of predation risk in affecting the choice of foraging patch selection in granivorous birds. Butler *et al.* (2005) showed that chaffinches given a choice between foraging in short or long stubble would prefer the short stubble until the ratio of food between the two patches was greater than 1:2.5, in favour of the high stubble. It has previously been shown that chaffinches had a 13% higher head-up vigilance period and 13% lower feeding rate when foraging in long stubble patches (Whittingham *et al.* 2004). It appears that the increased visual obstruction causes the birds to increase their vigilance levels to compensate with the resulting decrease in feeding rate. However, when the difference in prey density between two patches leads to an increase in feeding rate substantial enough to compensate for the increased vigilance it becomes profitable to switch to the obstructed patch. Note that when food densities are sufficiently high that the forager's feeding rate is approaching its maximum rate switching to an obstructed patch would never be more profitable. It is clear that anti-predator behaviour must be accounted for in patch selection (Robinson 1997) and functional response models that incorporate anti-predator vigilance

will be important in spatial depletion models where distribution and patch choice are important.

1.3.7 Competitive behaviour

Lastly, a complicating factor for many systems is interspecific competition and the detrimental effect of inferences competition and kleptoparasitism on feeding rates. For example, interference competition in shorebirds occurs through both prey depression, i.e. mobile prey retreating to safety on detection of a predator, and aggression from dominant foragers, which both increase with competitor density (Stillman & Goss-Custard 2010). However, although interference competition has often been found for groups of granivorous birds foraging on clumped seed (Johnson, Giraldeau & Grant 2001, 2006) this effect has not been found at lower densities (Smart *et al.* 2008) and is not expected to occur much in the wild. Partly this is because prey handling in granivorous birds is rapid due to the small size of each seed, thus allowing little time for kleptoparasitism (Brockman & Barnard 1979).

1.3.8 Parameter estimates: how accurate are published parameter values?

As previously described searching rates are difficult to measure and, therefore, most published searching rates are derived by fitting a functional response model (usually the Holling's disc model) to the observed feeding rate and estimating the searching and handling parameters. For such parameter estimates to represent observed values there is an assumption that the chosen model accurately describes the functional response of the species in question. As has been shown there are often violations of the model's assumptions and consequently these parameter

estimates are not truly estimates of the behaviour parameters. Goss-Custard *et al.* (2006) use a simple hyperbolic function to model the functional responses of shorebirds, where the assumptions of the disc equation are not appropriate.

$$F = \frac{aD}{(b+D)} \tag{3}$$

where F = feeding rate (prey s^{-1}), D = prey density, a = the asymptotic constant and b = the half asymptotic function. Using such a model has reduced confusion in this literature by not confounding fitted behavioural estimates with experimentally measured estimates of these parameters. This lesson should be learnt and applied to granivorous birds. Consequently, few reported searching rate estimates should be treated with any confidence and obtaining realistic estimates of searching rate should be a focus of future research (Stephens *et al.* 2003).

1.3.9 Conclusions: functional responses of granivorous birds

Overall the foraging behaviour of granivorous birds is no more complicated than that of the best studied vertebrate example, shorebirds. Shorebirds have several complicating factors that increase the complexity, such as foraging for active prey that can adapt behaviourally to the presence of a predator (Stillman *et al.* 2000b), searching for multiple prey with different characteristics (shellfish or burrowing worms), searching visually or using a tactile probing bill (Nebel, Jackson & Elner 2005), different handling techniques for different individuals on the same prey (i.e. stabbers and hammerers (Goss-Custard & Durell 1988)) and interference competition cause by long handling times and large differences in foraging efficiency (Stillman *et al.* 1996; Stillman *et al.* 2000). Thus, granivorous birds might

provide a good model system for studying basic vertebrate functional responses.

1.4 The behavioural approach to conservation

Predicting the response of populations to changes in resource availability is a vital tool for managing threatened and declining species (Bradbury *et al.* 2001; Stephens *et al.* 2003; Norris 2004; Sutherland 2006). Traditionally, population modelling approaches within ecology have been phenomenological, with parameters derived directly from empirical studies of specific populations (Stephens *et al.* 2003; Sutherland 2006). Whilst these approaches can provide detailed insights into population level processes (Norris 2004) it cannot be known how changes to the environment will affect each parameter (i.e. birth rate, mortality, recruitment) and their interactions (i.e. density dependence) (Sutherland & Norris 2002). This makes extrapolation to novel conditions difficult and seriously limits the utility of these approaches for conservation management (Bradbury *et al.* 2001; Sutherland 2006).

An alternative approach is to underpin the assumptions of the model with evolutionary theory by assuming that each individual strives at all times to maximise its fitness (Sutherland 1996; Norris 2004). Within this framework extrapolating population-level predictions to novel conditions is possible because the fitness maximising rules are always applicable. Here the difficulty lies in understanding how individuals interact with their environment and compete with other organisms for space and resources. These knowledge gaps can often be solved through experimental or observational studies at the individual or small group level (i.e. Sutherland & Ens 1987; Goss-Custard, Cayford & Lea 1998; Caldow *et al.* 1999; Durell 2000; Stillman *et al.* 2000a) and are more easily dealt with than estimating population-level parameters (Sutherland 1996). Such models are broadly

identified as 'behavioural-based models' because they are concerned with the behavioural response to the prevailing conditions, but within this designation lies a range of models encompassing the breadth of scale and complexity (Stephens *et al.* 2003). The awareness of behaviour-based models amongst ecologists has certainly increased (Grimm 1999), but their use in conservation management is still in its infancy.

The need to integrate behavioural and evolutionary theory with conservation management has long been noted (Curie 1996; Caro 1999; Blumstein & Fernandez-Juricic 2004). Buchholz (2007) proposed the use of Tinbergen's 'four questions' (Tinbergen 1963) as a framework for addressing biodiversity loss where animals are maladapted to rapid anthropogenic changes, thus, truly grounding conservation within the behavioural paradigm. However, it is carefully noted that a behavioural approach is not necessary or appropriate for all conservation problems. Caro (2007) suggests that the integration of behaviour and conservation management has not yet fulfilled its potential because the theoretical nature of the behavioural discipline is largely irrelevant to management problems. It is suggested that before trying to apply behaviour to conservation we should begin by assessing the conservation problem to determine whether a behavioural approach is necessary (Caro 2007).

A clear example of the application of behavioural knowledge to a conservation problem is the effects of habitat loss and resource removal (i.e. commercial harvesting of shellfish) on shorebirds and wildfowl populations (Stillman & Goss-Custard 2010). Initially, the problems were approached through the development of habitat association models, but these failed to account for changes in density-dependence and always assumed that the carrying capacity had been reached (Goss-Custard *et al.* 1995). This led to the development of daily ration

models (Gill, Sutherland & Norris 2001) and spatial depletion models (Sutherland & Allport 1994), the latter use ideal free distribution theory and assume that the foragers select the most profitable patch to maximise their feeding rate. However, such models often underestimate the amount of food necessary to support a population and, therefore, underestimate mortality (Stillman & Goss-Custard 2010). It was realised that interference competition, social hierarchies and individual variation in competitive ability could have a significant effect on the intake rate of these species (Stillman *et al.* 1996; Stillman *et al.* 2000). The development of individual-based models that could account for individual variability and the competition between forager logically followed (Goss-Custard *et al.* 1995a, 1995b; Clarke & Goss-Custard 1996; Stillman *et al.* 2000c). Thus, the current level of behavioural complexity represented in these models was arrived at through necessity and not through an *a priory* assumption.

There is potential for a similar approach to be applied to granivorous farmland bird conservation because of the shared attributes of the problem: namely, overwinter starvation due to food shortages (Stephens *et al.* 2003). However, whilst there appears to be great potential for the application of behavioural knowledge to this applied problem the degree of complexity required is unknown. The problem must be approached incrementally, much like the shorebird example (Stillman & Goss-Custard 2010), building a solid foundation of behavioural knowledge and resist the temptation to assume that the answer to one problem can be directly applied to another. Here I present the case for a behavioural approach to granivorous farmland bird conservation and discuss how the research should proceed.

1.4.1 The functional response in behaviour-based models

Linking food availability and abundance to over-winter mortality requires an understanding of the effects that foragers will have on the abundance of these resources (depletion) and how this will feed-back to affect the intake rate and foraging decision of the foragers. Depletion models range in complexity from simple daily ration models to complex individual-based simulation models, however, they all aim to predict the consequences of changes in resource abundance on population level parameters by understanding the behavioural processes that underlie these observed patterns. Whilst functional response models are not always a component of these depletion models many models do use a functional response to link prey abundance to predator intake rate.

Daily ration models aim to predict the number of forager-days supported by a given resource (Stephens *et al.* 2003) assuming that each forager removes a quantity of food equal to its 'daily ration'. This ration is calculated based on the energy density of the food resource and the daily energy requirements of an active forager adjusted for its digestive efficiency. Daily ration models have been successfully used to predict biomass depletion by geese (Inger *et al.* 2006) and the carrying capacity of staging sites for swans (Nolet, Gyimesi & Klaassen 2006). Within daily ration models the functional response can be used to predict the time required to deplete the resources (Nolet *et al.* 2006) or predict the give-up density (threshold density), which is the lowest density the foragers can feed whilst still achieving their minimum daily energy intake (Goss-Custard *et al.* 2003). Not all daily ration models use a functional response: Inger *et al.* (2006) predicted the daily ration based on the daily energy requirements, the energy density of the food and the assimilation efficiency of the forager.

When resource depletion occurs at different rates depending on spatially ex-

plicit differences between resources and site characteristics then this spatial element must be incorporated into the models. Goss-Custard *et al.* (2003) showed that spatial elements are only necessary when there are differential rates of additional food loss between patches or the relative profitability between patches vary temporally. Butler *et al.* (2010) found that their spatial depletion model of farmland granivores was most sensitive to uncertainty in daily seed survival probabilities and as these could easily differ between patches there might be a need for the spatial component in such models. The inclusion of spatial elements into depletion models allows for density dependent effects and variation in patch quality, with foraging decisions based on maximising intake rate and ideal free distribution theory (Sutherland 1996). Several spatial depletion models have used the Holling's disc equation to predict the intake rate of the foragers as a function of the changing prey density (Butler *et al.* 2010; Lourenco *et al.* 2010), or used a variation on this model (Sutherland & Anderson 1993; Robinson 1997; Gill, Sutherland & Norris 2001; Nolet & Klaassen 2009).

If there exists significant individual variation in foraging ability, dominance status, susceptibility to interference or any other behavioural parameter that has consequences for survival then it might be necessary to incorporate such variations into the model. Caldow *et al.* (1999) incorporated individual variation in foraging efficiency into their models of oystercatchers foraging for mussels after showing that this parameter affected the use of supplementary feeding habitats. Shorebirds individual-based models have tended to use the interference-free instantaneous intake rate to predict the feeding rate of a bird as a functional of prey density: the model used is similar to equation 1.3.8.

1.4.1.1 A comment of threshold densities

Behavioural-based models often include a minimum threshold density below which a forager is unable to consume enough food to meet its minimum daily energy requirements (Goss-Custard *et al.* 2003). This value could be obtained from field observations of the minimum densities used by foragers (i.e. Gill *et al.* 2001), however, it is difficult to determine whether the patch is being avoided solely because of food depletion or in combination with other factors, i.e. predation risk, making other patches more desirable. Several studies have estimated the threshold density based on the rate at which food can be consumed given the time available for foraging (Goss-custard *et al.* 2003; Butler *et al.* 2010). This method often produces biologically implausible estimates of the threshold densities because under normal circumstances foragers are not time-constrained and, therefore, theoretically can spend much longer searching for food items than they would naturally. Butler *et al.* (2010) predicted that the threshold density for yellowhammers feeding on cereal crop seed was 0.53 seed m^{-2} . However, this contrasts starkly with the minimum densities that birds have been observed to give up on a crop (Moorcroft *et al*. 2002). The former value might represents a theoretical minimum which has been overestimated by field studies because food in surrounding fields was not exhausted. However, such decrepencies highlight the caution that must be taken when using estimates of threshold densities predicted from functional response models.

1.5 Functional response models and the conservation of granivorous birds

1.5.1 Demographic trends of granivorous farmland specialists

Recent changes in land management have caused a sharp decline in the abundance and range of a number of species, many of which are strongly associated with farmland in the UK (Chamberlain *et al.* 2000; Newton 2004). Farmland bird species have declined in abundance more than any other group of birds in the UK over the last 30 years, and the farmland habitat appears to be strongly associated with these declines (Fuller *et al.* 1995; Proffitt *et al.* 2004). Whilst many generalist granivorous birds have increased in abundance granivorous farmland specialist have all suffered substantial declines (Fuller *et al.* 1995; Siriwardena *et al.* 1998).

Since the publication of several key papers showing the population trends for UK farmland birds in the period from the late 1960s (Fuller *et al.* 1995; Siriwardena *et al.* 1998) there has been a concerted effort to reverse these declines, especially after the adoption by the UK Government of a Public Service Agreement to reverse these declines by 2020. Whilst there have been a few successes, largely for targeted schemes aimed at specific species (Kleijn & Sutherland 2003; Bradbury *et al.* 2004; Hinsley *et al.* 2010), the broader schemes have yet to deliver the anticipated results (Davey *et al.* 2010). Consequently, the picture presented over a decade ago for farmland bird populations has not changed significantly and most granivorous farmland specialists are still not showing signs of a recovery (Defra 2010).

1.5.2 Causes of the declines: the late winter 'food gap'

Of the farmland bird species that have undergone population declines over the last 30 years there is much variation in life-history traits, taxonomy and ecology, although most granivorous specialists have been effected to some extent, several suffering large population declines (Fuller *et al.* 1995). The patterns of decline of UK farmland birds cannot be explained by any single factor, and declining species do not fall strongly into discrete groups according to a particular ecological or environmental factor that is effecting them (Siriwardena *et al.* 1998). Siriwardena *et al.* (1998) showed that specialization, i.e. farmland or generalist, was the only important life-history trait or ecological characteristic that could explain the changes in abundance. Whilst most species that are largely dependent on farmland have declined in abundance since the late 1960's, most generalist species have shown an increase (Siriwardena *et al.* 1998; Fuller *et al.* 1995).

Newton (2005) suggests eight components of agricultural intensification that have had some negative effect on farmland bird populations, including: increase in agro-chemical use; removal of semi-natural habitat (i.e. hedgerows); temporal changes in sowing and harvesting regimes; land drainage; homogenisation of the agricultural landscape; and higher stocking densities in uplands areas. For granivorous farmland birds the main cause of the population declines has been the reduction in food availability, especially over-winter, which has resulted in low adult survival (Newton 2005). The increased use of herbicides with the consequent reduction in weed seeds and the loss of seed-rich habitat, such as arable land and stubble fields, are primarily responsible (Siriwardena, Baillie & Wilson 1999).

Siriwardena, Calbrade & Vickery (2008) found that peak use of over-winter food supplementation for yellowhammers occurred from February onwards sug-

gesting that there is a supply/demand gap that needs to be filled. When over-winter food supplementation has been targeted towards granivorous birds the local response has been positive (Hinsley *et al.* 2010). The provision of winter bird food patches have been shown to not only increase the use of these patches by granivorous species but to also increase the number of breeding territories (Hinsley *et al.* 2010). The UK cirl bunting *Emberiza cirlus* population has increased substantially since 1989, when the UK population numbered 118 pairs, and this is in part due to the prevision of a winter food supply, provided through the framework of the Countryside Stewardship Scheme (Peach *et al.* 2001).

1.5.3 Functional responses and the recovery of granivorous farmland birds

As described in section 1.4, models underpinned by evolutionary theory can be used to predict the affect of environmental changes on population persistence. The functional response has been shown to be central to many such models (section 1.4.1) and, therefore, a thorough understanding of the functional response of these species is required before confidence can be place in models based on their estimates of intake rate. Because the population-limiting parameter for granivorous farmland birds is often starvation due to a supply/demand gap in over-winter food supplies the similarities with shorebirds conservation lends support to the behavioural-approach. Here, as for shorebird conservation, the main questions to be addressed are those that have a direct conservation or management implication. These include:

- How much food is required to support the desired population density?
- When will the available food supplies be exhausted at the current popula-

tion density of the foragers?

- How will interventions designed to bridge the supply/demand gap affect population persistence?

These questions are difficult to address satisfactorily with demographic models because there is no way of relating food abundance or density-dependence to the demographic rates unless the population has been studied under such conditions previously (Sutherland & Norris 2002). Because we are interested in a quantitative question regarding the rate of resource depletion for a given density of foragers the behavioural approach offers a potentially fruitful approach to quantifying the individual demand for food and the rate of its consumption (Bradbury *et al.* 2001). This is largely because the rate of resource consumption will undoubtedly vary with the prevailing environmental conditions and this will not only affect the depletion rate but could induce time-constraints on the foragers resulting in starvation. The point at which density-dependent effects begin to induce mortality in the population can be surprising. Goss-Custard *et al.* (2003) showed that Oystercatchers *Haematopus ostralegus* L require 6 – 8 times the density of shellfish than predicted by simple ration models because of the effect of individual variation and interference competition on subdominant foragers.

1.6 Concluding statement

Whilst there is much knowledge regarding the foraging behaviour of granivorous birds mechanistic descriptions of these behavioural processes have not been fully integrated into functional response models of these species. There is potential for adaptive behaviours (i.e. handling time and searching rate affected by prey density), anti-predator vigilance, satiation and many more factors to be important

in shaping the functional response of these foragers. Few studies have implicitly tested the ability of simple functional response models to predict the observed feeding rate of granivorous birds and, therefore, there is an over-reliance on the Holling's disc model. The development and thorough testing of functional response models tailored to the behaviour of these foragers might lead to better predictive models and greater insight into the foraging behaviour of these species.

1.7 Thesis objectives

The objectives of this thesis are to address the knowledge gap surrounding the mechanistic understanding of the foraging behaviour of granivorous birds. I aim to identify overlooked behaviours and interactions and derive new functional response models that provide more accurate representation of the observed foraging behaviour. I hope that such advances will help to increase the understanding of the foraging behaviour of granivorous foragers and also contribute towards behavioural-based models of these species, providing a more accurate model to link resource availability to feeding rate. The objectives are defined as follows:

OBJECTIVE 1 – To test the ability of mechanistic functional response models to predict the observed feeding rates of granivorous farmland birds.

OBJECTIVE 2 – To identify violations of the assumptions of basic functional response models of granivorous farmland birds.

OBJECTIVE 3 – To develop new functional response models that account for the limitations in existing models.

OBJECTIVE 4 – To test the assumptions of the new models and suggest the future progression of research into the functional responses of these species

Specific hypotheses will be defined in the chapter introductions after a full exposition of the subject.

The functional response models in this thesis are tested following Holling's 'experimental component analysis'. Foraging experiments are used to measure the behavioural parameters for each model and the model's ability to describe the observed functional response judged only using these parameter values; this provides the only true test of a mechanistic model.

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Chapter 2

The effect of habitat complexity on the functional response of granivorous passerines

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2.1 Abstract

1. Recent population declines of granivorous farmland birds have been associated with reduced overwinter survival due to reductions in food supply. An important component of predicting how food shortages will affect animal populations is to measure the functional response, i.e. the relationship between food density and feeding rate, over the range of environmental conditions experienced by foragers. Crop stubble fields are an important foraging habitat for many species of granivorous farmland bird. However, some important questions remain regarding farmland bird foraging behaviour in this habitat, and in particular the effect of stubble on farmland bird functional responses is unknown.

2. I measured the functional responses of a species of granivorous passerine (chaffinch) consuming seeds placed on the substrate surface in three different treatments: bare soil, low density stubble and high density stubble. I measured the behavioural parameter of searching rate, handling time and

several metrics of vigilance (proportion of time, frequency and duration of scans) to determine the mechanism through which a reduction in feeding rate due to habitat structure occurs. Additionally, I tested the ability of several functional response models to predict the observed functional response from experimentally measured behaviour parameters.

3. Stubble significantly reduced feeding rates, but there was no significant difference between the two stubble treatments. Stubble reduced feeding rates by reducing the maximum attack distance, i.e. the distance over which an individual prey item is targeted and consumed. Several negative non-linear trends were found in handling time per seed and the proportion of time spent vigilant, but the searching speed, duration of vigilances bouts and duration of head-down search periods were unaffected by the presence of stubble. The frequency of vigilance bouts was higher in the bare soil treatment, but this is likely to be a consequence of the increased feeding rate.

4. I show the influence of a key habitat type on the functional response of a granivorous passerine, and discuss the consequences for predicting the functional response of these species and for predicting the effect of environmental change on farmland bird populations.

2.2 Introduction

The populations of many species of farmland birds have declined significantly over the past four decades (Fuller *et al.* 1995; Siriwardena *et al.* 1998; Gregory *et al.* 2004). These declines have been mirrored by a broad loss of biodiversity within the agricultural landscape (Chamberlain *et al.* 2000; Robinson & Sutherland 2002) and have been linked strongly with the intensification of the UK agricultural industry (Donald *et al.* 2001). Many granivorous passerine species utilise agricultural land at some time during the year (Robinson & Sutherland 1999), but it is those species that are most strongly associated with farmland, such as the corn bunting *Miliaria calandra* L and yellowhammer *Emberiza citronella* L, that have undergone the most significant declines in abundance (Siriwardena *et al.* 1998; Newton 2004). The direct causes of these declines vary between species, but for granivorous farmland specialists the reduction in the winter seed supply

has had the most significant impact (Hole *et al.* 2002; Moorcroft *et al.* 2002; Siriwardena *et al.* 2008).

Environmental planning and policy decisions, that are required to reverse these declines and prevent further losses to biodiversity, need to be based on informed scientific opinion if they are to be effective. There are many potential approaches to predicting the effects of ecological changes within the farmland environment (Stephens *et al.* 2003; Sutherland 2006), but behaviour-based models that predict population survival from foraging behaviour are under-pinned by evolutionary theory, assuming that a forager maximises its fitness at all times, and therefore enable predictions to be made for novel conditions (Norris 2004; Sutherland 2006). Such models have previously been used to predict the effects of environmental change on coastal bird populations (Stillman & Goss-Custard 2010) and have been used to guide management decisions and policy to the benefit of species of conservation concern (Caldow *et al.* 2004; Goss-Custard *et al.* 2004; Durell *et al.* 2008). The potential for such models to predict the effect of environmental changes on populations of farmland bird species has been noted (Bradbury *et al.* 2001) and several preliminary studies have been conducted to assess the suitability of the approach to this habitat (Stillman & Simmons 2006; Smart *et al*. 2008). To-date several spatial depletion models have been developed for birds within the farmland habitat (Robinson 1997; Butler *et al*. 2010) although the behavioural assumptions of these models are simple and have not been well tested.

A key component of these models is the functional response (Stillman & Simmons 2006), i.e. the relationship between prey density and feeding rate (Soloman 1949), as it links resource density to population dynamics (Sutherland 1996). The functional response is affected by both behavioural and environmental factors, such as seed type, seed distribution, and habitat structure. Although the functional response has now been measured for several granivorous farmland passerines feeding on bare substrate (Robinson 1997; Robinson 2003; Smart *et al*. 2008), it is necessary to understand how the functional response varies over the range of environmental conditions experienced by foraging birds. Stubble fields are an important foraging environment for many species of granivorous farmland bird (Gillings *et al*. 2005). However, despite a range of studies in this area (Butler & Gillings 2004; Butler *et al*. 2005a; Butler *et al*. 2005b) there are still some important gaps in our knowledge, in particular the effect of stubble on farmland

bird functional responses over a broad range of seed densities is unknown.

Previously, increasing habitat complexity has been shown to significantly reduce the mobility of chaffinches *Fringilla coelebs* L during foraging (Butler & Gillings 2004) and stubble height has been shown to affect the proportion of time chaffinches spent vigilant (Butler *et al*. 2005b). Longer stubble has been shown to cause a significant reduction in the feeding rate due to an increase in the proportion of time spent vigilant (Whittingham *et al*. 2004). Whittingham and Markland (2002) found intake rates and search times of canaries *Serinus canarius* L were significantly faster on an earth substrate compared to grass, even when the seeds contrasted better with the grass. They suggested that the most likely causal mechanism was the increased surface area that the birds were forced to search resulting from the structure of the grass. Even with this apparent reduction in feeding rates, it has been shown that chaffinches will choose to forage in obstructed habitats if the seeds are easier to find, i.e. more conspicuous or more abundant, than in a less obstructed environment (Butler *et al*. 2005b; Jones *et al*. 2006). It is therefore important to determine not only whether the presence of stubble brings about a reduction in feeding rate, but at what seed density any such reduction occurs and the mechanism through which it occurs. Understanding this is key from a conservation perspective as any reduction in feeding rate at low seed densities will be of consequence for the survival of individuals when food becomes scarce.

The aim of this study was to: (i) experimentally determine whether the presence of crop stubble influenced the functional response of a medium size granivorous passerine, the chaffinch; (ii) determine the behavioural mechanisms underlying any effect of stubble on the functional response; and (iii) to test the ability of several functional response models to predict the observed functional response for experimentally measured behaviour parameters. It is our hypothesis that the presence of stubble will reduce feeding rate (the number of prey consumed per unit time) at low seed densities as it creates a physical obstruction to movement and visibility, and that this effect will be magnified by higher stem densities. I measured the influence of seed density and habitat type on feeding rate, and six parameters that can influence feeding rate: handling time (the time taken to consume one prey item), the proportion of time spent vigilant (and hence not feeding), the frequency of vigilance bouts, the duration of time spent with the head-down (i.e. searching), the search speed and the prey attack distance (the last

two parameters in combination determining the area of habitat searched per unit time). I discuss the consequences of our results for farmland bird conservation.

2.3 Methods

2.3.1 Study system

The study site was on a farm at the Royal Society for the Protection of Birds (RSPB) reserve at Arne, Dorset, UK ($50^o42'$N, 2^o2'W). The farm is surrounded by improved grassland, with two large areas of wild bird crops that attract a large flock of chaffinches throughout the winter. Birds are regularly fed with rapeseed at two sites adjacent to the study area, which attracted the birds onto the site throughout the winter. The flock size peaked in January and February 2008, with approximately 150 chaffinches, 20 goldfinches *Carduelis carduelis* L, 20 greenfinches *Carduelis chloris* L and 3 bramblings *Fringella montifringilla* L. The chaffinch was chosen for this study as it is a medium-size granivorous finch, forms large flocks in winter, predominantly feeds on the ground and is easily attracted to an area if food is regularly provided. As such the chaffinch is a good model species for studying the foraging behaviour of this group of birds.

2.3.2 Field experiments

A purpose-built feeding platform was used to mimic the natural foraging environment of the birds and provide an unobstructed view so that their foraging behaviour could be filmed. The platforms were constructed to mimic three foraging conditions encountered by wild birds: bare soil, low density stubble (60 stems m^{-2}) and high density stubble (120 stems m^{-2}). The feeding platforms were constructed from 1 x 1 m wooden boards onto which several fine layers of soil were glued (PVA waterproof glue). The central 0.5 x 0.5 m section of the bare soil platform was marked by a 5 cm nail in each corner and a smaller nail half-way along each side which provided a reference point for measuring distances. The stubble platforms were made by sliding 13 cm lengths of stubble onto 10 cm wires inserted through holes drilled in the platform. The stubble was positioned in parallel rows 12.5 cm apart at a density of 60 (low density) and 120 (high density) stems m^{-2}. These values were also chosen to represent naturally occurring conditions (Butler & Gillings 2004; Whittingham *et al*. 2004).

The platform was set flush to the ground to allow easy access to birds foraging in the adjacent grass. A 2 x 2 m nylon ground-sheet placed under the platform allowed spilt food to be swept up from the immediate surroundings. The platform was placed 1 m from a small vegetated embankment under some overhanging trees, adjacent to a wire fence. A constant supply of food was provided by two bird feeders and a second feeding platform placed a short distance from the experimental platform, which were regularly topped up with rapeseed, rape tailings or wild finch seed mixes. A photographic hide (www.wildlifewatchingsupplies.com, medium dome hide) was set up 4 m from the front edge of the platform adjacent to the fence and remained in place throughout the fieldwork in order to minimise disturbance to the birds. From the hide, the birds were filmed using a Canon XL1 video camera mounted on a tripod and set to a height of 1 m above the platform. Birds were fed on the feeding platform for a two month period before the experiments began, allowing them to adjust to the experimental set up. Rapeseed was used throughout the study as it proved most attractive to the chaffinches and is planted extensively throughout England. The seed densities used were 25, 50, 100, 200, 400, 800 and 1600 seeds m^{-2}, and were chosen so that the emphasis was on the lower densities, which are representative of densities found generally in arable fields (Robinson & Sutherland 1999; Moorcroft *et al.* 2002). Birds could not be attracted reliably to the platform when the seed density was < 25 seeds m^{-2}. Seed densities up to 800 seeds m^{-2} were counted by hand, but the highest density was estimated from average seed mass. Three trials were conducted for each of the seed densities between 200 and 1600 seeds m^{-2} for each of the three habitat conditions. In order to minimise the effect of depletion at the lower three seed densities, more trials were conducted (n = 5 or 6 for 25 & 50 seeds m^{-2}, n = 4 for 100 seeds m^{-2}) and only the first few birds to feed in each trial were considered in the analysis (see below).

Because of the logistics of setting up each new platform, there was no within-day randomisation between platform types, only between the seed densities. The experiments were conducted between 28 January 2008 and 12 February 2008, in the following order: low density stubble; bare soil; high density stubble. It was necessary to repeat some of the bare soil trials after the high density stubble experiments were completed in order to supplement the data. During the study period, food was placed on the platforms and the feeders topped up between 08:00 h and 08:30 h, and the first trial would begin at 09:00 h. The trials were stopped

by 16:30 h when the light levels were too low to obtain good video footage. At the beginning of each trial, a randomly-allocated seed density would be spread out on the platform and filming would begin. The trial would continue until at least five birds had consumed a minimum of five seeds each at the densities above 200 seeds m^{-2} and at least three birds had consumed five seeds each at the lower densities. The minimum interval between trials was maintained at 10 minutes throughout in order to reduce the disturbance to the birds.

Two potential problems encountered during this study were pseudo-replication and the effects of satiation. Pseudoreplication was a potential risk between trials as the birds were disturbed during the setting up of each experiment and thus individuals could not be tracked. However, due to the large size of the flock, the turnover of individuals feeding on the experimental platform was high and so the potential for pseudoreplication was minimised. Furthermore, the number of birds surrounding the platform was monitored during the experiments and movement on and off the platform occurred frequently. The potential for satiation to affect the feeding rates of the birds is a further potential problem, but as the birds increase their risk of predation when feeding on the platform they are likely to try to minimise their time foraging in the open regardless of the level of satiation. The effect of the time-of-day at which the experiments took place was included in the analysis. These problems will always be encountered in field experiments, but I attempted to minimise them in the choice of study system, experimental design, selection of focal individuals and statistical analysis.

2.3.3 Video analysis

The videos were downloaded to a computer and analysed using a purpose built event recorder. For each trial above 200 seeds m^{-2} the first five birds to complete five consecutive pecks, i.e. without interrupting the foraging behaviours of searching, handling and vigilance, were chosen for behavioural analysis. For the lower densities up to three birds per trial were used for behavioural analysis and care was taken to select birds that foraged in different areas of the platform to minimise the effect of depletion. Although individual birds could not be identified during each trial every effort was made to keep track of birds that had fed on the platform and if the individual returned to the platform the time and position of the bird was recorded so that it would not be included twice in the analysis.

Feeding rate was measured for five consecutive pecks to obtain an average

feeding rate for each individual. The measurement began at the video frame before the first seed was touched by the bird's bill and ended the frame before the fifth seed was touched, thus covering four search-capture sequences. Handling time is the time it takes the individual to handle each food item and was measured from the frame at which the bird picked up a seed to the frame at which the bird stopped manipulating the seed in its bill. Because this relied on the bird's bill being visible on camera it was not always possible to obtain the handling time from five consecutive pecks, so a minimum of three consecutive pecks was used. The proportion of time spent vigilant whilst foraging was measured over the five consecutive pecks and calculated as the proportion of the time during which the bird's bill was orientated in parallel or at a greater angle to the soil, a behaviour that could be clearly identified on the videos. Similarly, the frequency of vigilance bouts (i.e. number of head-up bouts per second) and the head-down time (i.e. the time interval between the bill dropping below horizontal and the detection of a seed) were measured over 5 consecutive pecks, with the bill parallel to the ground or at a greater angle considered as being vigilant.

Distances were measured using a purpose built grid placed on the computer monitor, which allowed the 2-dimensional movements of the birds to be measured accurately. This method was tested prior to the study and found to be accurate to ± 3.3 % of the observed value (see Fig. 2.1). The distances were measured from the foot nearest to the camera or, if the bird was facing the camera, between its feet. Searching speed was calculated by measuring the distance travelled in a continuous straight movement, divided by the time taken to travel this distance. Three searching speeds were measured for each individual bird, and mean searching speed was calculated from the searching speeds at the lower two densities as at higher seed densities the birds moved less frequently. Only search speeds measured over one or more seconds were included in the statistical analysis, as estimated searching speed was found to be highly variable when measured over a shorter time interval. Food attack distance was measured as the distance between the position of the bird when it targeted a prey item, signalled by direct movement towards the item, and the position of its bill when pecking the prey item. The maximum attack distance for each bird was estimated as the maximum distance of three feeding events. Within each trial, mean attack distance was calculated as the mean of the maximum attack distances estimated for each bird.

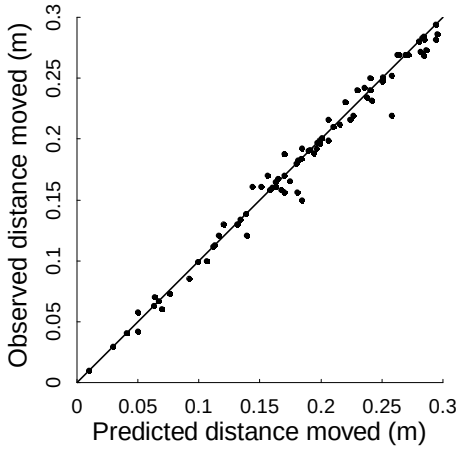

Figure 2.1: A test of the method used to measure the distances moved by foragers on the feeding platform. An model bird was moved to randomly generated coordindate positions on the foraging platform and the distance measured using a grid placed over the screen. The predicted results are compared here against the real (observed) distance moved and shown to have an error of ± 3.3 %.

2.3.4 Predicting the functional response

Two different models were used to predict the functional response from measured behavioural parameters as they had previously been shown to provide a good fit for the observed functional response (Smart *et al.* 2008). Model 1 is the Holling's disc equation:

$$F = \frac{aD}{1+aDH} \qquad \text{Model 1}$$

where F = feeding rate, a = searching rate, D = prey density and H = handling time. Search rate was calculated as $a = 2ds$, where d = attack distance (in previous papers referred to as detection distance, e.g. Stillman & Simmons 2008; Smart *et al.* 2008) and s = searching speed (Stillman & Simmons 2006). Model 2 is derived from the Holling's disc equation (Smart *et al.* 2008), but includes vigilance and allows for vigilance and handling to occur simultaneously:

$$F = \begin{cases} (1-v)aD & if\ D \leq \frac{v}{(1-v)aH} \\ \frac{aD}{1+aDH} & if\ D > \frac{v}{(1-v)aH} \end{cases} \qquad \text{Model 2}$$

where v = proportion of time spent vigilant.

2.3.5 Statistical analysis

General linear models were used to determine the significance of the relationship between each behavioural parameter and the habitat and seed density. Initially, the interaction term (habitat * seed density) was included, but in all cases this interaction was non-significant and therefore the term was removed from the analyses presented in this paper. Seed density was transformed (natural log) so that a linear model could be used to analyse the relationship between feeding rate and seed density. The statistical analysis was completed using SPSS 15.0. and R.2.10.1 (R Development Core Team 2009)

2.4 Results

2.4.1 Does stubble density influence the functional response?

There was no effect of habitat on feeding rate between the two stubble densities (b = 0.034, $t_{210} = 0.481$, $P = 0.631$), so these data were combined before comparison with the bare soil treatment (b represents the slope of the regression model). Both habitat, i.e. bare soil or stubble (b = 0.049, t_{316} = 4.254, $P < 0.001$) and seed density (b = -0.197, t_{316}= 5.937, $P < 0.001$) were found to affect the feeding rate of the chaffinches. There was a positive relationship between feeding rate and seed density in both habitat treatments, and the mean feeding rates in the bare soil treatment were consistently higher than those in the stubble treatment (Fig. 2.2). Two subsequent analyses were performed to determine whether these results were affected by the time of day at which the experiments were conducted or the number of other birds (competitors) on the feeding platform. In both analyses, habitat (P = < 0.001) and seed density (P = < 0.01) significantly affected the feeding rate, but neither the time of day ($P = 0.788$) nor the number of competitors (P = 0.712) had any significant affect on feeding rate.

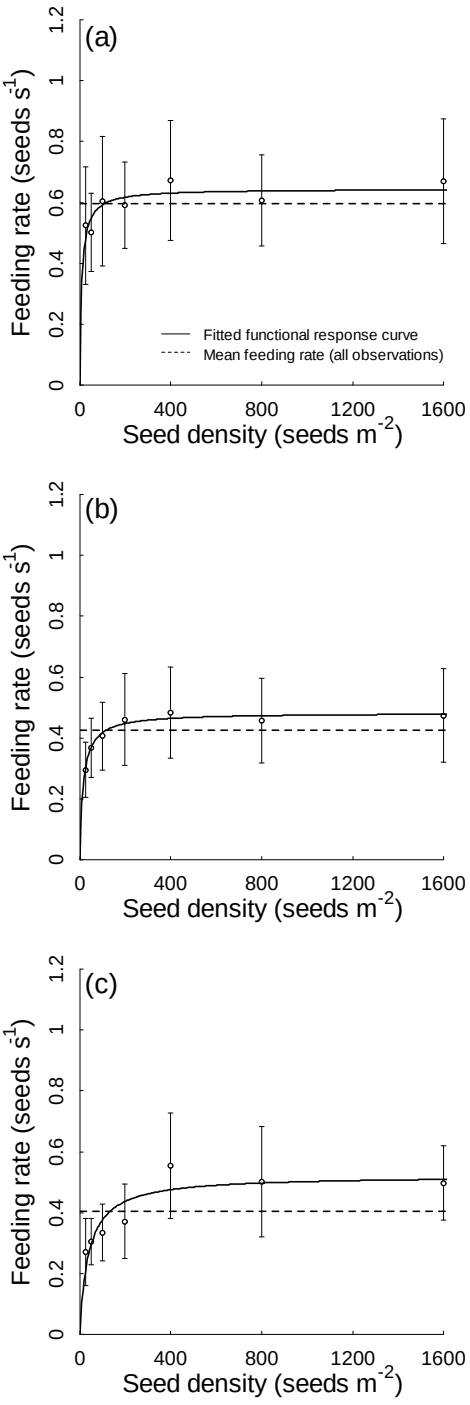

Figure 2.2: The mean observed feeding rates of chaffinches feeding at different densities of rapeseed (with associated 95% confidence intervals) under different habitat conditions: (a) bare soil, (b) low density stubble, (c) high density stubble. The lines were fitted using the slope and intercept derived from a LM after natural log transformation of seed density value (see text for details).

2.4.2 What are the mechanisms underlying the effect of stubble density on the functional response?

Natural log transformed handling time (Fig. 2.3a) was positively correlated with log(seed density) in the bare soil (b = 0.091, t_{102}= 2.833, P = 0.006) and untransformed handling time (Fig. 2.3c) was negatively correlated with log(seed density) in the high density stubble treatments (b = -0.464, t_{102}= -0.052, P = 0.0298); there was no correlation in the low density stubble treatment (Fig. 2.3b) (b = -0.00005, t_{99}= -0.333, P = 0.74).

The proportion of time spent vigilant (Fig. 2.4) was significantly positively correlated with log(seed density) in the bare soil treatment (b = 0.035, t_{103}= 3.306, P = 0.0013) and the high density stubble treatment (b = 0.027, t_{99}= 2.505, P = 0.014); there was no correlation in the low density stubble treatment (Fig. 2.3b) (b = 0.000005, t_{103}= 0.192, P = 0.848). There was no sigificant difference between in the proportion of time spent vigilant between to two stubble treatments (b = 0.04, t_{203}= 1.919, P = 0.056) and therefore these data were combined and compared to the bare soil treatment. However, there was no significant difference between the proportion of time spent vigilant in bare soil or stubble (b = 0.00007, t_{308}= 0.004, P = 0.997).

It has previously been shown that the frequency of vigilance bouts (head-up rate) (Cresswell *et al.* 2003) and the duration of vigilance bouts (Whittingham *et al.* 2004) can influence the ability to detect a predator and, therefore, might be altered to compensate for a visual obstruction. The frequency of vigilance scan (Fig. 2.5) was not correlated with seed density for the bare soil treatment (b = -0.018, t_{103}= -0.872, P = 0.385), low density stubble treatment (b = 0.000007, t_{103}= -0.192, P = 0.848) or high density stubble treatment (b = 0.00002, t_{103}= 0.688, P = 0.493). There was no significant difference between the frequency of vigilance scans in the two stubble treatments (b = 0.02, t_{202}= 0.741, P = 0.459) and so they were combined for comparison with the bare soil treatment. There was a significant difference between the frequency of vigilance scan in the bare soil and stubble treatments (b = -0.094, t_{307}= -3.379, $P < 0.001$).

The natural log transformed duration of vigilance (Fig. 2.6) scans were not significantly correlated with seed density in either of the treatments; bare soil (b = 0.00009, t_{103}= 0.713, P = 0.478), low density stubble (b = 0.0001, t_{103}= 0.635, P = 0.527) and high density stubble (b = 0.00007, t_{98}= 0.621, P = 0.536). There

was no significant difference between the duration of vigilance scans in the two stubble treatments (b = 0.058, t_{202}= 0.731, P = 0.465) and so they were combined for comparison with the bare soil treatment. There was no significant difference between the duration of vigilance scan in the bare soil and stubble treatments (b = -0.138, t_{307}= 1.854, P = 0.065).

Furthermore, I analysed the head-down search time (Fig. 2.7) as this has previously been shown to be related to response times in chaffinches (Whittingham *et al*. 2004). There was no correlation between head-down search time (squared root transformed in both stubble treatments) and seed density in any of the treatments; bare soil (b = -0.0002, t_{103}= -1.378, P = 0.171) low density stubble (b = 0.00004, t_{103}= 0.66, P = 0.511) and high density stubble (b = 0.00003, t_{98}= 0.422, P = 0.674).There was no significant difference between the square root transformed head-down search time in the two stubble treatments (b = 0.056, t_{202}= -0.934, P = 0.352) and so they were combined for comparison with the bare soil treatment. There was no significant difference between the head-down search time in the bare soil and stubble treatments (b = -0.019, t_{307}= -0.505, P = 0.614).

Both searching speed and attack distance were only measured at the lowest two seed densities, as higher seed densities resulted in shorter movements by the birds and this does not represent the maximum attack distance and searching speed. There was no significant difference between the searching speeds at 25 and 50 seeds m^{-2} in bare soil (t-test, t_{28}= 0.629, P = 0.534), low density stubble (t_{24}= 1.336, P = 0.194) and high density stubble (t_{18} = 0.685, P = 0.502) treatments, and therefore the searching speeds at each density were combined for each experimental condition. There was no significant difference between the searching speed in the two stubble treatments (b = -0.012, t_{45}= -1.314, P = 0.196) and so they were combined for comparison with the bare soil treatment. There was no significant difference between the searching speed in the bare soil and stubble treatments (b = -0.019, t_{75}= -1.94, P = 0.056), although approaching significance (Fig. 2.8).

Maximum attack distance (Fig. 2.9) provides a measure of the accessibility, both visually and physically, of food items to the forager. Although the stubble habitat will not influence attack distance parallel to stubble rows, the stubble greatly reduces the potential of detection and attacks across rows, and consequently the birds are forced to make shorter foraging 'attacks' between the stubble stems. There was no significant difference between the maximum attack

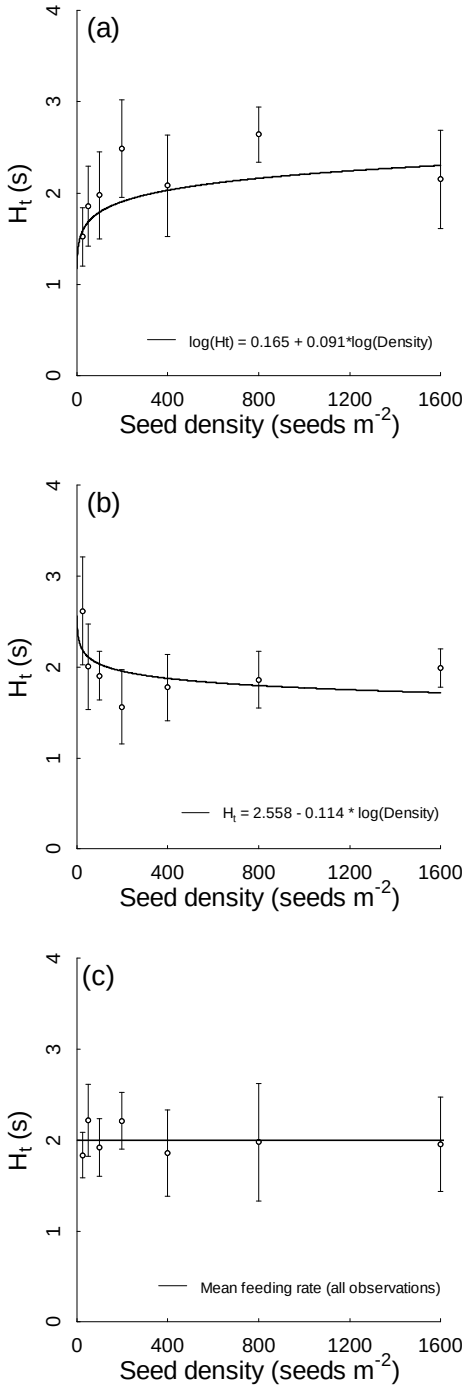

Figure 2.3: The mean observed handling time of chaffinches feeding at different densities of rapeseed (with associated 95% confidence intervals) under different habitat conditions: (a) bare soil, (b) low density stubble, (c) high density stubble.

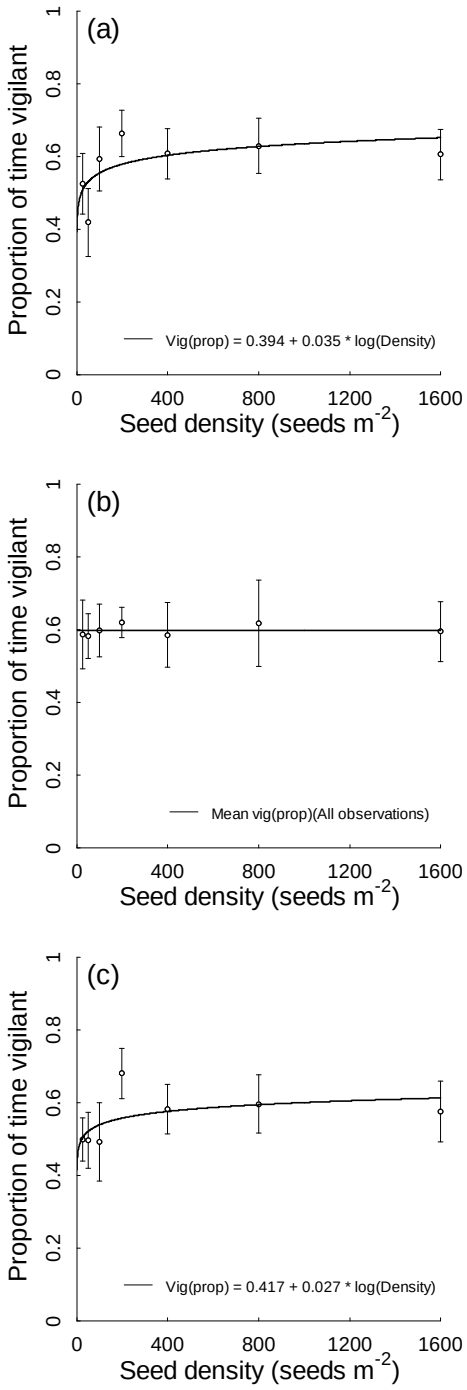

Figure 2.4: The mean proportion of time spent vigilance for the chaffinches feeding at different densities of rapeseed (with associated 95% confidence intervals) under different habitat conditions: (a) bare soil, (b) low density stubble, (c) high density stubble.

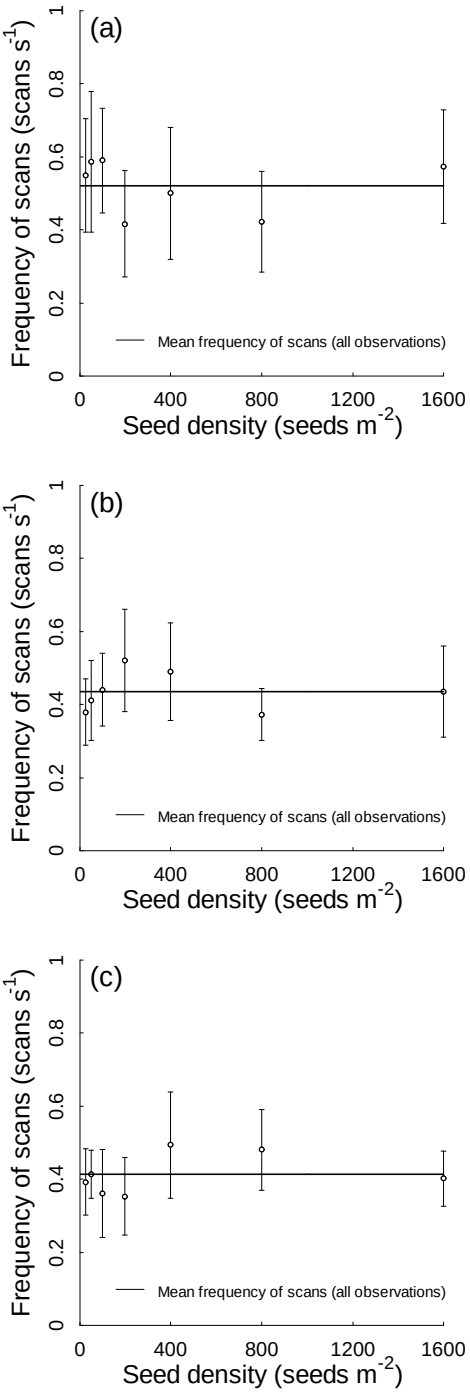

Figure 2.5: The mean observed frequency of vigilance scans of chaffinches feeding at different densities of rapeseed (with associated 95% confidence intervals) under different habitat conditions: (a) bare soil, (b) low density stubble, (c) high density stubble.

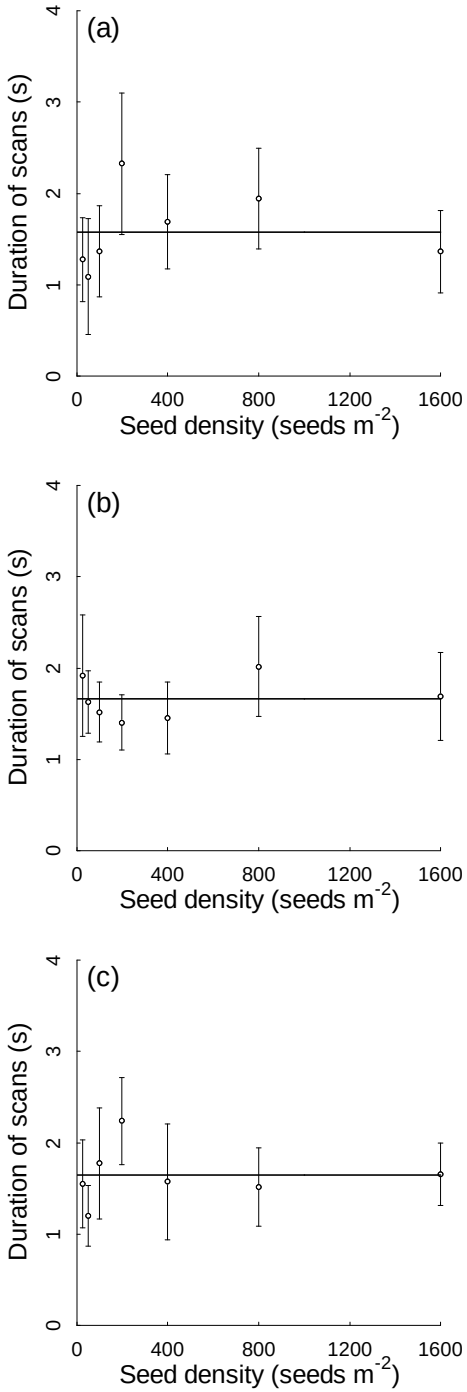

Figure 2.6: The mean observed duration of vigilance scans of chaffinches feeding at different densities of rapeseed (with associated 95% confidence intervals) under different habitat conditions: (a) bare soil, (b) low density stubble, (c) high density stubble.

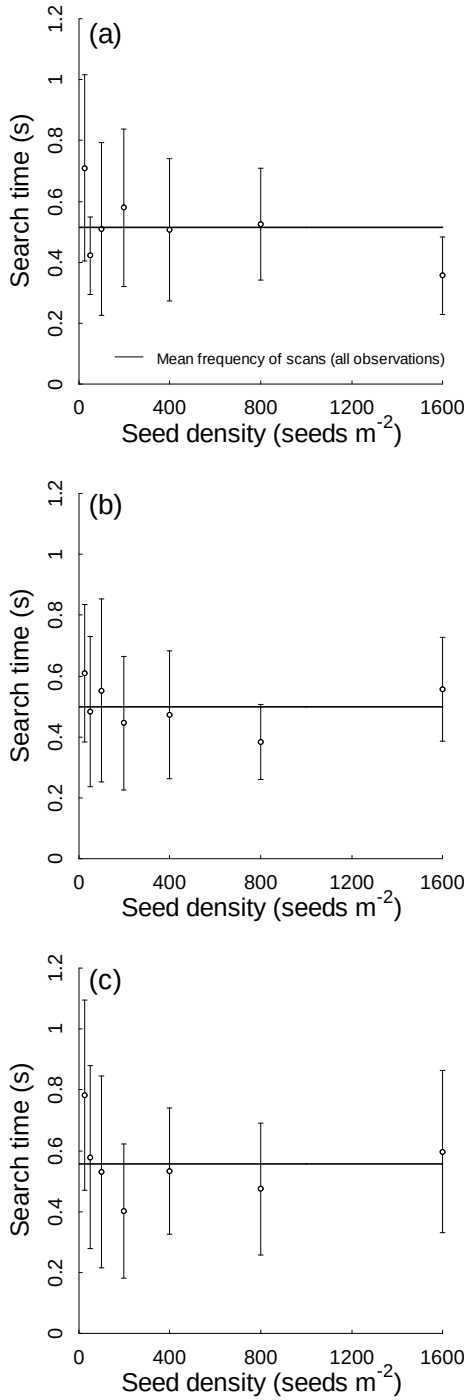

Figure 2.7: The mean observed searching time of chaffinches feeding at different densities of rapeseed (with associated 95% confidence intervals) under different habitat conditions: (a) bare soil, (b) low density stubble, (c) high density stubble.

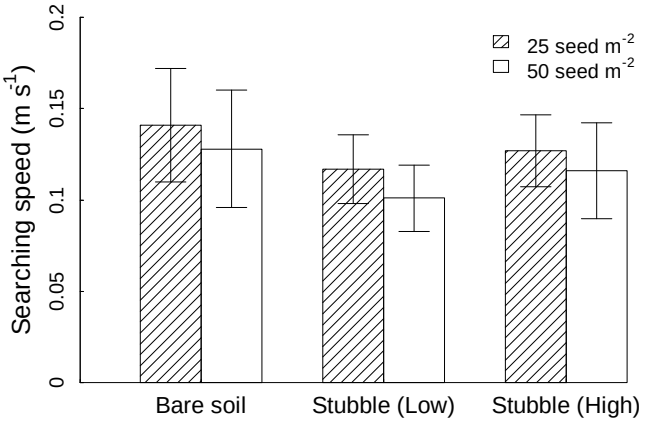

Figure 2.8: The mean observed searching speed of chaffinches (with associated 95% confidence intervals) measured at the two lowest seed densities.

distances in the two stubble treatments (b = -0.002, t_{51}= -0.248, P = 0.805) and so they were combined for comparison with the bare soil treatment. The maximum attack distance was significantly lower in the stubble treatments (b = -0.04, t_{60}= -4.181, $P < 0.0001$) and the attack distance was negatively correlated with seed density (b = -0.0008, t_{80}= -2.1, P = 0.039).

2.4.3 Predicting the functional response from behavioural parameters

Equation 1 and Equation 2 were tested for their ability to predict the functional responses based on experimentally measured behavioural parameters (Table 2.1; Fig. 2.10). These two equations have previously been shown be suitable for describing the functional response of a granivorous passerine (Smart *et al.* 2008). Equation 1 provided a good estimate of the maximum feeding rate for the two functional responses in stubble, low density stubble (R^2= 0.03) and high density stubble (R^2= 0.1), but consistently underestimated maximum feeding rate in the bare soil treatment (R^2= -0.2). Equation 2 produced an identical fit to equation 1 in all cases, indicating that the proportion of time spent vigilant was not sufficient to influence feeding rate (assuming that vigilance and handling can occur simultaneously). The high variability in the feeding rate at all prey densities caused the R^2 values to be low, however, these are comparable to those found in other studies (Smart *et al.* 2008)

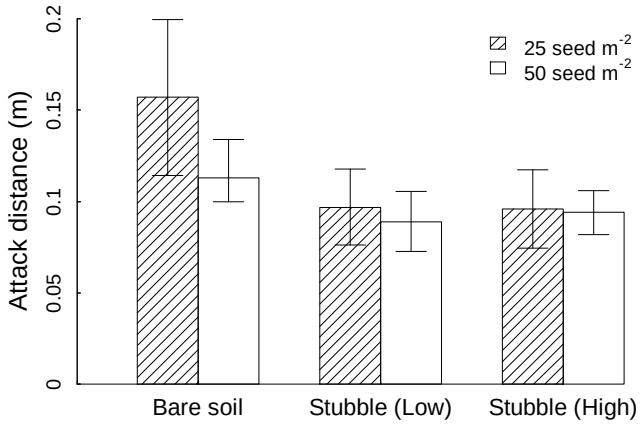

Figure 2.9: The mean observed maximum attack distance of chaffinches (with associated 95% confidence intervals) measured at the two lowest seed densities.

	Bare soil (±95% CI)	**Stubble 1 (±95% CI)**	**Stubble 2 (±95% CI)**
Habitat structure			
Stubble density (stubble m^{-2})	0	60	120
Behavioural parameters			
Handling time (h) (prey s^{-1})	1.919±0.094	1.823±0.072	1.989±0.077
Vigilance (v) (proportion of time)	0.578±0.015	0.598±0.014	0.559±0.015
Duration of vigilance bouts (s)	1.57±0.261	1.689±0.206	1.655±0.217
Head-up time (s^{-1})	0.582±0.129	0.431±0.051	0.403±0.090
Head-down time (s)	0.544±0.111	0.631±0.102	0.656±0.153
Search speed (s) ($m\ s^{-1}$)	0.131±0.016	0.113±0.013	0.122±0.011
Maximum attack distance (d) (m)	0.136±0.03	0.095±0.015	0.098±0.008
Search rate (a) ($a = 2ds$)($m^2 s^{-1}$)	0.0357	0.0215	0.0239

Table 2.1: The observed behavioural parameters for each of the described habitat conditions. The table shows the mean for each parameter across all seed densities for which it was measured as no significant relationship was found between these behavioural parameter and seed density.

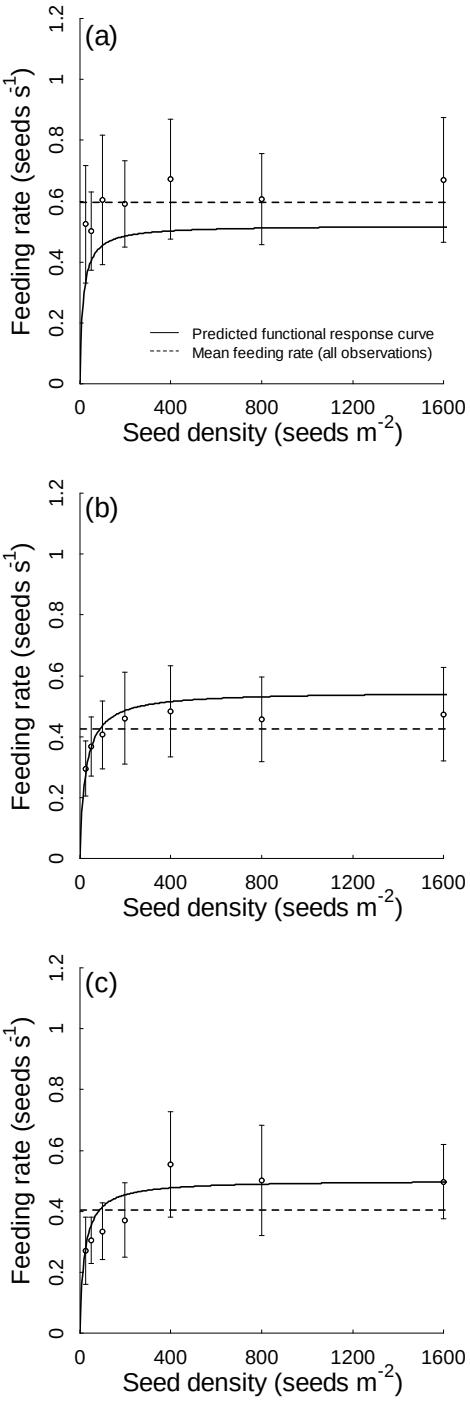

Figure 2.10: The functional response predicted using the Holling's disc equation (equation 1) using the observed values for search rate and handling time (see Table 1). The mean feeding rates (with associated 95% confidence intervals) are shown under different habitat treatments: (a) bare soil, (b) low density stubble, (c) high density stubble.

2.5 Discussion

To predict the effects of environmental change on farmland bird populations we must understand how foraging behaviour, and specifically the functional response, of these species is affected by the foraging environment. Thus far, the effect of habitat complexity (e.g. the presence of stubble) on farmland bird foraging behaviour has typically been investigated over a limited number of food densities (Butler & Gillings 2004; Whittingham *et al.* 2004; Butler *et al.* 2005b). This is understandable, as these studies were not designed to explicitly measure the effect of habitat on the functional response. However, a key question remaining is, how do environmental factors influence the shape of the functional response, particularly at low resource densities, which needs to be known if the effect of food shortages on survival are to be predicted. Those functional responses that have been measured for farmland birds have been measured in simple environments, e.g. bare soil (Robinson 1997; Smart *et al.* 2008). In this study I adapted a technique developed previously for measuring the functional response of a farmland bird under simple conditions (Smart *et al.* 2008) to mimic the more complex habitat of a stubble field.

This study shows that the presence of stubble causes a decrease in feeding rates and that this is due to a reduction in the accessibility of food items which reduces the area searched over time by the forager. Searching speed and maximum attack distance are both components of searching rate (the area searched for prey per unit time) for a species that exhibits a continuous foraging behaviour, i.e. searching whilst moving. However, here I showed that the area searched is reduced only through a reduction in the maximum attack distance and not a reduction in the searching speed. A similar result was found for canaries foraging on a grass substrate, which resulted in an increase in the searching time when compared to an earth substrate without causing a physical obstruction to the birds' movements (Whittingham & Markland 2002). At low seed densities the feeding rate is limited by the time it takes to find each food item, thus the decrease in the accessibility of food items reduces the searching rate and consequently reduces the feeding rate (Butler & Gillings 2004). Feeding rate was higher in the bare soil treatment even at high seed densities. This may have been due to the small and infrequent movements that birds make even when the seed density is very high and which are obstructed in stubble treatments. These movements appear to be

due to the birds becoming more selective when food is highly abundant and easily accessible, although some movements may be subtle attempts to guard their resource or to avoid competition (DJB pers. obs.).

The bird's searching speed was not significantly different between the three habitats because they tended to follow the lines of the stubble when foraging and thus the stubble did not interfere with their movement. Butler *et al*. (2004) found that chaffinches exhibited more one-dimensional foraging patterns in long stubble, whereas in short stubble a two-dimensional foraging pattern was observed. However, another study found no difference in bird mobility between stubble heights (Whittingham *et al*. 2004). The effect of stubble on the mobility of the birds is likely to be greater in this study as the stubble treatments were compared with bare soil, a habitat that provides no obstruction, rather than two stubble heights; short stubble still provides obstruction to movement and vision, even if the effects are reduced in relation to long stubble. Thus the effect of stubble on the foraging movements of the birds is to inhibit the mobility of the birds, i.e. decreasing their choice of foraging pattern, but not to affect the speed at which the birds move through the habitat. It was common for birds to detect seeds in adjacent rows, at right-angles to their direction of travel, and move sideways to consume to these seeds from between the stubble stems. This explains the reduction in attack distances between the bare soil and stubble treatments, where the presence of stubble prevents the long diagonal approaches to food items which occur unimpeded on bare soil.

The head-up rate was found to be significantly higher in the bare soil treatments, but as vigilance is most often carried out in parallel with handling time this is likely to reflect the higher feeding rates and not necessarily an increase in vigilance (Cresswell *et al*. 2003). The proportion of time spent vigilant and the head-down time, parameters that could influence feeding rates, were not significantly affected by the habitat structure. Chaffinches rely on visual detection of an approaching predator and upon detection they retreat to nearby cover. Visually obstructions caused by surrounding vegetation, i.e. stubble, might lead to an increase in the time allotted to vigilance, and thus reduce the feeding rate. Whittingham *et al*. (2004) found a 13% decrease in peck rates in long stubble compared with short stubble and concluded that this was due to increased vigilance and not changes in the amount of time spent searching. Conversely, Butler *et al*. (2004) found no significant differences between vigilance (head-up rates) and

habitat structure (long:long vs. long:short stubble). This suggests that the local habitat structure is only one variable that influences a bird's perception of danger and, therefore, the proportion of time it allotted to vigilance. Here the feeding platform was positioned close to cover and the birds were in a large flock, which may have helped reduce the perceived predation risk (Cresswell 1994; Barta *et al*. 2004). Previous studies have largely been conducted with lone birds (Cresswell 2004; Whittingham *et al*. 2004; Butler *et al*. 2005b) and this may explain the differences observed here. Situating the feeding platforms within a different local environment, such as open ground far from cover, may produce a different pattern of vigilance, such that the chaffinches increase their vigilance in the stubble.

There is much variation in the handling times of finches and buntings within the literature (Stephens *et al*. 2003), which might reflect the difficultly of measuring such parameters in wild birds. The mean handling times measured here were consistent with handling times previously measured for granivorous birds (Robinson 2003; Smart *et al*. 2008) and were not affected by the presence of stubble. However, there was considerable variation in the handling times measured throughout the experiments and the lack of consistency by individual birds suggests that this was not due to individual differences. These variations may have been caused by differences in the seed hardness or seed quality, i.e. poorer quality seeds that may be quickly discarded. Given its importance, further study will be necessary to determine the effects of environmental and species differences on handling time. Interference competition can result in a significant reduction in the feeding rate at high competitor densities, when food is aggregated, and when handling time is long. Bird density did not affect the feeding rate in this study, probably due to the widely distributed food and quick handling times. Some competitive behaviour was observed, such as dominant individuals chasing others from the feeding platform, although most of the time individuals were well spaced within the feeding area avoiding competitive interactions.

It has previously been shown that the Holling's disc equation and a second equation, derived from the disc equation but incorporating vigilance, are suitable models for predicting the functional response of granivorous farmland birds (Smart *et al*. 2008). Here I tested the ability of these two equations to predict the functional response from observed behavioural parameters. The results showed that under these conditions the inclusion of vigilance (overlapping vigilance and

handling) had no effect on the model's predictions because the proportion of time spent handling was relatively large (as seeds were captured rapidly), allowing vigilance to occur during handling. This is also evidence that the time allocated to each vigilance bout was shorter than handling time. Under conditions where vigilance bouts are longer than handling time and searching times are long (reducing the proportion of time spent handling), vigilance is likely to become an important parameter. The Holling's disc equation provided a good fit for the functional responses in stubble predicting the maximum feeding rate, but did not predict the functional response well in the bare soil treatment. Here the observed feeding rates were consistently higher than those predicted based on the observed behaviour parameters and this might be due to the large variation in the handling time and adaptive behaviour. Such adaptive behaviour can be seen in Fig. 2.3a and b where the parameters vary with prey density and, consequently, an average handling time calculated from across the functional response does not represent the underlying behaviour and provides a poor prediction of the overall functional response. Such adaptive behaviour has been commented on previously (Hassell *et al*. 1976; Abrams 1990; Smart *et al*. 2008) but is often over-looked in functional response models.

Habitat complexity has been shown here to affect the functional response of a granivorous passerine and this has implications for the conservation of threatened farmland specialists. At a fixed seed density, feeding rate was lower in the stubble treatments than in the bare soil treatment. The birds benefited from a simpler foraging environment that allowed them to forage in a more efficient manner. Jones *et al*. (2006) has shown that chaffinches are willing to spend more time foraging in obstructed habitats if food is easier to locate here than in unobstructed habitats. Similarly, Butler *et al*. (2005b) has shown that chaffinches will favour foraging in long stubble over short stubble when the seed density is more than two times greater. For species such as chaffinches that use visual cues to detect predators, a simpler habitat is likely to reduce the predation risk and provide further benefit to the birds. Although chaffinches are not a threatened or declining species they share foraging characteristics with several declining granivorous farmland birds. For example, Butler *et al*. (2005a) showed that granivorous birds as a functional group preferred to forage on plots with shorter stubble, whereas two other granivorous farmland birds, Skylarks *Arvensis arvensis* and partridge *spp.*, preferred plots with higher stubble. However, a comprehensive study and com-

parison of the foraging behaviours of granivorous farmland bird species would be helpful in discerning similarities and differences between these species.

Developing predictive models for the farmland habitat is of increasing importance due to the declining status of many species of farmland bird. Given some important gaps in our knowledge of the foraging behaviour of these species, parameterising these models is difficult and more research is required to address these gaps. This study has demonstrated a technique for measuring the functional responses of granivorous farmland birds, thus providing a means to build-up a detailed knowledge of their foraging behaviour under a variety of conditions. This is crucial for the development of behavioural-based models for farmland birds, which must incorporate differences in foraging behaviour brought about by the environment if they are to accurately predict the effect of environmental changes on these species.

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Chapter 3

Vigilance and the functional response of granivorous foragers

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3.1 Abstract

1. Functional response models that predict the relationship between feeding rate and food density often include only two behavioural parameters, handling time and searching rate. However, vigilance can occupy a large proportion of foraging time and, consequently, may affect the functional response. Previous functional response models of granivorous birds showed no effect of vigilance on predicted feeding rates; these models assumed that all of handling time is compatible with vigilance and, therefore, overestimated the potential time for cost free vigilance to occur.

2. Here I have derived a new functional response model that incorporates the proportion of time spent vigilant (v) and the proportion of handling time that is compatible with vigilance (p). This model allows for the relationship between vigilance and handling to vary from completely compatible to mutually exclusive, and degrees in between.

3. To determine whether vigilance can affect the functional response of a granivorous bird, grey partridge *Perdix perdix* L, I measured the functional response and associated behavioural parameters, and used the behavioural estimates to parameterise the model. Any deviation from the feeding rates predicted using a model without vigilance indicates that vigilance is affecting the predicted functional response.

4. I found that vigilance only affected the predicted functional response at very low prey densities (< 3 seeds m^{-2}). Simulations show how the potential for vigilance to affect feeding rate (i.e. the values of p given v) increases as v increases. I parameterised the model using data from chaffinches *Fringilla coelebs* L, which were shown to spend > 50% of their foraging time vigilant, and found that even with a high value of p vigilance reduced feeding rates at higher seed densities.

5. This study shows that vigilance can affect the feeding rate of a granivorous bird when either the proportion of time spent vigilant is high or the proportion of compatible handling time is low. This may affect larger scale ecological processes, i.e. spatial distribution of foragers and patterns of resource depletion, as individuals try to mitigate the effects of vigilance by maximising their feeding rate whilst minimising their predation risk.

3.2 Introduction

Functional response models used to describe the relationship between feeding rate and prey density (Sutherland 1996) often simplify foraging behaviour into only two components, searching rate and handling time. These models, most notably the Holling's disc equation (Holling 1959), assume that searching rate limits feeding rate at low prey densities, when prey is harder to find, but handling time becomes more limiting as prey density increases. However, anti-predator behaviours, including vigilance, are a major component of foraging (Treves 2000) and have been shown in some species to occupy a high proportion of foraging time (Baker, Stillman & Bullock 2009; Smart, Stillman & Norris 2008; Fernandez-Juricic & Beauchamp 2008; Inger *et al.* 2006). Under some conditions, vigilance could become the major factor limiting feeding rate and, consequently, affecting the functional response. To-date, attempts to incorporate

the proportion of time spent vigilant into functional response models of granivorous birds have provided no significant improvements in the models predictive power (Smart *et al.* 2008; Baker *et al.* 2009), however, these models have not accounted for some key implications stemming from the interaction between handling and vigilance.

The relationship between vigilance and other components of foraging behaviour, including searching (Whittingham & Markland 2002), handling (Cowlishaw *et al.* 2004) and group size (Beauchamp 2008), has been the subject of much research and several reviews (Bednekoff & Lima 1998; Beauchamp 2009; Treves 2000). Beauchamp (2009) describes two types of vigilance for foragers in a group, vigilance aimed at other group members and vigilance aimed at detecting predators, and suggests that these two types of vigilance will either have no relationship with prey density or a negative relationship. For vigilance aimed at detecting predators a negative relationship is observed when the foragers are at risk of starvation (McNamara & Houston 1992), a scenario common to declining granivorous farmland birds throughout Europe (Hole *et al.* 2002; Siriwardena, Calbrade & Vickery 2008). For granivorous birds, vigilance is assumed to primarily occur during the head-up phase of foraging and several studies have suggested that the head-up rate is positively correlated with predator detection (Whittingham *et al.* 2004; Cresswell *et al.* 2003). It is typical for granivorous bird species to handle their prey in a head-up posture (Butler *et al.* 2005b; Johnson, Giraldeau & Grant 2001; Smart *et al.* 2008) and, therefore, simultaneous handling and vigilance is possible.

Handling time, defined as the total time taken to capture and consume one prey item (Stephens & Krebs 1986), also includes components that are not compatible with vigilance, i.e. approaching and picking up the prey item, and this distinction might be crucial to understanding the affect of vigilance on the functional response. Cowlishaw *et al.* (2004) showed that the ratio of compatible handling time to searching time can be used to predict when vigilance might cause a decrease in feeding rate, such that when this ratio is high vigilance has no effect on feeding rate. Searching time is often assumed to be a function of prey density (Stephens *et al.* 1986) and, therefore, if compatible handling time is constant the effect of vigilance on the feeding rate should be negatively correlated with prey density. The relationship between prey density and vigilance in both birds and mammals appears to be mixed (Beauchamp 2009), however, some re-

sults might be influenced by factors other than prey density i.e. interference from conspecifics. At high prey densities, when handling time is limiting feeding rate, the extent of the overlap between vigilance and compatible handling time is crucial in determining the effect of vigilance on the feeding rate (Smart *et al.* 2008). Other evidence (Cowlishaw *et al.* 2004) suggests that when the compatible handling time is short relative to searching time, and vigilance is long, vigilance will begin to limit feeding rate, thus affecting the shape of the functional response.

Smart *et al.* (2008) developed three separate functional response models that incorporated vigilance, each allowing different overlap between vigilance, searching and handling. However, two different studies (Smart *et al.* 2008; Baker *et al.* 2009) found no improvement in the ability to predict the functional response of a granivorous bird from observed behavioural parameters using these models. This happened because the models assumed that vigilance could occur throughout the whole of handling time, whereas some components of handling (e.g. approaching prey) could be incompatible with vigilance. Consequently, these models overestimated the potential time for cost free vigilance to occur. It is also possible that the prey densities used in these studies were not low enough to reduce the searching time to a sufficient degree to observe any effect of vigilance on feeding rate. For these reasons, any effect of vigilance on the functional response may not have been detected in these studies. Fortin *et al.* (2004) derived a functional response model that could estimate the 'spare time' during foraging that could be allocated to vigilance behaviour, however, they did not incorporate vigilance into the functional response model. To address these problems I have developed a new functional response model that allows the proportion of handling time that is compatible with vigilance to vary. Depending on its parameter values the new model can represent each of the models derived by Smart *et al.* (2008) (model 1 (Holling's disc equation) – no vigilance; model 2 – no overlap between handling and vigilance; model 4 – complete overlap between handling and vigilance), as well as the continuum between these extremes.

In this study I have: (i) derived the new functional response model; (ii) measured the functional response and associated behavioural parameters (i.e. total handling (H_t), the proportion of compatible handling time (p), searching rate (a) and the proportion of time spent vigilant (v)) of a granivorous bird, the grey partridge *Perdix perdix* L (Fig. 1); (iii) parameterised the new functional response model for grey partridge to predict when vigilance will affect the functional re-

sponse; and (iv) tested the model on a previously studied species, the chaffinch *Fringilla coelebs* L, that spends >50% of its foraging time vigilant, to test the implication of higher vigilance on the functional response. If vigilance affects the functional response there will be a reduction in feeding rate relative to that predicted by a model that excludes vigilance. To maximise the potential to detect an effect of vigilance on the functional response I required a forager that handles prey quickly, but still spends a large proportion of its foraging time vigilant. The grey partridge has been show to spend ~40 % of its foraging time vigilant (Watson, Aebischer & Cresswell 2007), which is broadly similar to previously studied granivores (Smart *et al.* 2008; Baker *et al.* 2009), but it handles seeds more rapidly and, therefore, has less potential for cost-free vigilance during handling. Furthermore, I manipulated the searching rate by reducing the lower prey densities to levels below those used previously and through altering the habitat structure (Whittingham & Markland 2002; Baker *et al.* 2009), i.e. two treatments: bare soil and crop stubble. I discuss the implications of this study for predicting the functional responses of granivorous foragers and in the broader understanding of foraging behaviour.

3.3 Methods

3.3.1 Study species and site

The grey partridge is a farmland game bird that predominantly feeds on plant material, including seeds, during the winter (Holland *et al.* 2006). This species is significantly larger (i.e. grey partridge mass = ~390 g; corn bunting mass = 42 – 53 g) than the previously studied finches and buntings, but has broadly similar foraging behaviours, i.e. continuous foraging, visual detection of prey and foraging bouts divided between searching, handling and vigilance. This species has previously been shown to spend ~40% of its foraging time vigilant (Watson *et al.* 2007) and preliminary trials found that they handled wheat seeds faster than corn buntings *Miliaria calandra* L (Smart *et al.* 2008).

This study was conducted on the rearing fields at the Game & Wildlife Conservation Trust, Fordingbridge, Hampshire, in southern England. Twenty five eight-week old grey partridges were purchased from Heart of England Farms (Warwickshire, UK) on 18th September 2008 and were divided up into five ran-

Figure 3.1: Grey partridge *Perdix perdix* L (Photograph by Peter Thompson, used with permission)

dom groups of five birds, individually colour-ringed (Flat coil (FC) size 3 (8mm)) and placed into housing pens. Outside of the experimental period (i.e. 14:00 until 08:30) the birds were fed ad libitum food (until 12 weeks of age a high protein pellet Keepers Choice Mini Rearer and subsequently Keeper's Choice Maintenance Pellets and wheat) and throughout the experiments they had constant access to water. The birds were attended daily by experienced game keepers to assure they remained in good health.

3.3.2 Behavioural observations

Each group was housed in two interconnected pens, constructed from 3 x 1.5 m prefabricated wooden framed wire mesh panels, one used for housing and the other for the experiments. The 3 m^2 pens were arranged in a 5 x 2 grid, with an interconnecting hatch between the front and back pen. The pens were roofed with a fine mesh and each had a door to provide access. During the experiments the birds were unable to see the birds in neighbouring pens as groups not being studied were shut temporarily in the housing pens. The housing pen had a grass surface, two sources of shelter (tree branches and a wooden ledge) and a water supply. Each experimental pen was fitted with a black ground sheet to remove any natural sources of food and to allow any spilt food to be swept up. A 1.5 m^2 experimental platform, built from three 1 x 0.5 m plywood boards attached to a wooden frame, was placed centrally in each pen. The stubble platforms were constructed similarly, but with the addition of stubble stems glued in place. The stubble stems were spaced 10 cm apart along each row and 25 cm apart between

neighbouring rows and the stubble was cut to a height of 13 *cm*. This height (Butler, Bradbury & Whittingham 2005a) was chosen to reflect values found naturally, however, the spacing was chosen from field tests to provide maximum physical obstruction without directly impeding the bird's movement, i.e. without pushing the stubble over.

The functional response was measured across eight seed densities (5, 10, 15, 25, 50, 100, 200, 400 seeds m^{-2}) with one replicate per group of birds for each of the seed densities above 25 seeds m^{-2}. At high densities, once on the feeding platform the birds spread out to forage simultaneously on undepleted sections of the platform. However, at low densities ($\leq$ 25 seeds m^{-2}) the first few individuals to start feeding on the platform would quickly consume all the available seeds. Therefore, several replicates were required to film all the individual birds foraging at these densities. This was repeated for both the bare soil and stubble treatments. The food was removed from each pen one hour before the start of each experiment at the beginning of the day, with the first experiment starting at 09.30, thus giving the birds some time to feed before the experiment. This was important for both the welfare of the birds and because I did not want to measure the feeding rate of starving birds, which would represent an extreme condition. There was a one hour interval between each experiment throughout the study in order to maintain a consistent level of hunger. Four replicates were conducted on each pen per day, with each replicate taking not more than four minutes. The seed densities and treatments were fully randomised for each group throughout, but in order to maintain even spacing between the replicates the group order was randomly chosen anew each day.

For each replicate, 1125 cm^3 of pre-sieved soil was spread evenly across the platform, giving a depth of 5 *mm*; onto this the appropriate number of wheat seeds were randomly scattered. Wheat seeds were chosen for the experiment as they had been used previously to measure the functional response of a granivorous passerine (Smart *et al.* 2008), but were known to be handled more rapidly by grey partridge. The birds were filmed from a Canon XL1 video camera (www.canon.co.uk) placed 1.5 *m* from the front edge of the platform (outside of the pen) and at a height of 1 *m* above the platform. Filming was started immediately upon set up and continued until each bird had made six or more (three or more at < 25 seeds m^{-2}) consecutive pecks or until significant depletion of seeds had occurred across the whole platform. At all densities I was careful to focus

on foraging bouts that occurred on previously unused portions of the platform so that depletion would not affect the observed feeding rate. Very few aggressive interactions were observed between the birds throughout the experiments, with all individuals feeding undisturbed on the experimental platform.

3.3.3 Video analysis

The videos were downloaded and analysed using a purpose built event recorder that allows frame by frame viewing. The feeding rate was measured from the frame before the first peck until the frame before the last peck for a minimum of six pecks at seed densities above 15 seeds m^{-2} and a minimum of three pecks for the lowest two densities, although most recorded foraging bouts were longer. Handling time was divided into two components based on the compatibility with vigilance. The incompatible component (H_x) was measured from the time at which the bird began moving towards the target seed, shown by a distinct change in behaviour, to the frame before contact with the target. The compatible component (H_c) was measured from contact with the target seed until the seed was consumed. The proportion of compatible handling time (p) was calculated in relation to the total handling time (H_t), i.e. $H_x + H_c$.

Blanchard & Fritz (2007) emphasised the importance of distinguishing between routine and induced vigilance, as the latter had significantly more affect on the feeding rate. Here I consider routine vigilance only and any feeding bout that was interrupted by an obvious external stimulus was excluded from the analysis. Vigilance was defined by the head being in upright position with the bill parallel to, or directed away from the ground. Although it has been previously demonstrated that birds can remain partially vigilant whilst foraging (Lima & Bednekoff 1999) this is difficult to quantify. By using this definition I am measuring the vigilance of the birds when they are fully vigilant, which gives a good measure of their perceived threat levels. The proportion of time spent vigilant (v) was calculated as the proportion of time displaying vigilant behaviour during the foraging bout. The frequency of vigilance was measured as the number of times the head was raised into a vigilant position during each foraging bout. The length of vigilance bouts was measured as the mean time spent with the head in a vigilant position for each bird. Searching time measures the amount of time an individual spends searching for a prey item before detection. Here I define searching time as the time spent with the head angled below 90^o regardless of the posture (upright

or head-down), and I include both stationary and active searching under this definition: this was measured from the frame at which searching resumed until the frame before detection. Most detection events occur to either side of the bird's head and so detection events are characterised by a sudden change in direction and often an increase in speed.

Both attack distance and searching speed required an accurate measure of the distance moved by the birds across the screen. This was accomplished by importing a screen capture of the start and finish position of the bird into Photoshop CS4 (www.adobe.com). A 15 x 15 cell grid layer was placed over the top of the video images and the grid was warped using the perspective tools to fit over the shape of the platform. The coordinates of the bird's position on the platform could now be accurately read from the grid with an error of ± 3.1%, as calculated using a model bird moving between random coordinates on a 1.5 m^2 platform 3.2. The attack distance was defined as the distance between the target seed and the bird at the point that movement towards the seed was initiated. Searching speed was calculated from the movement along a straight line when the bird was actively searching. For both maximum attack distance and search speed only the lowest three seed densities were used as movement becomes less frequent at higher seed densities. The ability to detect prey items can be influenced by many environmental factors, including the distance to the prey item, the ambient lighting conditions, contrast of prey with background, as well as forager specific factors, such as height and visual acuity. Thus, searching rate is the most complex of the behavioural parameters to quantify and several models have been derived that incorporate estimations of many of these complex factors. However, I choose to define searching rate based upon a simple model with parameters that can be easily quantified, which gives an approximate estimation of the area searched by the forager. The area searched is approximately twice the maximum distance over which prey items were observed to be taken (i.e. the bird can search over the same distance on either side), multiplied by the distance travelled: thus, $a = 2ds$, where d = attack distance and s = searching speed (Stillman & Simmons 2006; Fortin *et al.* 2004).

3.3.4 Alternative functional response models

The Holling's disc equation (Model 1) describes a Type II functional response using just three parameters, a = searching rate, H_t = handling time and D = prey

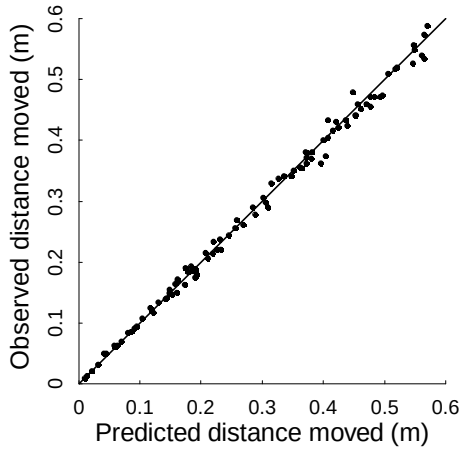

Figure 3.2: A test of the method used to measure the distances moved by foragers on the feeding platform. An model bird was moved to randomly generated coordindate positions on the foraging platform and the distance measured using a grid placed over the screen. The predicted results are compared here against the real (observed) distance moved and shown to have an error of ± 3.1 %.

density, and assumes that searching and handling are mutually exclusive events:

$$F = \frac{aD}{1+aDH_t} \qquad \text{Model 1}$$

Previously, this model has been shown to provide the best predictions of observed functional responses from experimentally derived values of a and H for granivorous passerines (Baker *et al.* 2009; Smart *et al.* 2008).

Model 2 (see Appendix 1 for derivation) is a new functional response model that incorporates both the proportion of time spent vigilant (v) and the proportion of handling time that is compatible with vigilance (p). In this functional response model, handling and vigilance can be mutually exclusive or compatible behaviours, and any degree of overlap between p and v is reflected in the predicted feeding rates (3.3).

$$F = \begin{cases} \frac{(1-v)aD}{1+(1-p)aDH_t} & if\ \frac{1}{D} \geq \frac{(p-v)aH_t}{v} \\ \frac{aD}{1+aDH_t} & if\ \frac{1}{D} < \frac{(p-v)aH_t}{v} \end{cases} \qquad \text{Model 2}$$

These models were parameterised using the observed behavioural values (Ta-

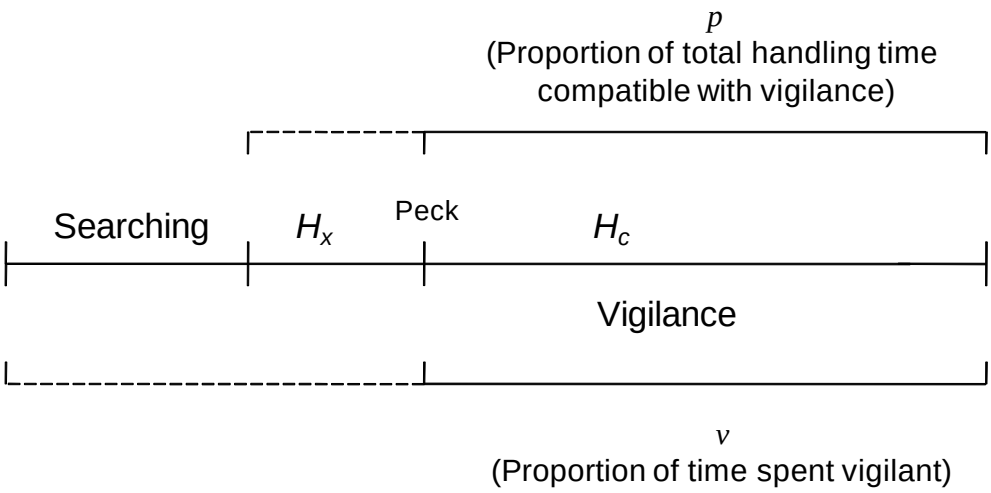

Figure 3.3: Diagramatic representation of the foraging sequence of a granivorous forager as represented by Model 2.

ble 3.1) for grey partridge foraging on wheat seeds in both bare soil and stubble treatments. The models were compared using Akaike Information Criterion (AIC).

3.3.5 Statistical analysis

All statistical analysis was completed using R 2.9.0. (R Development Core Team 2009) and the nlme package (Pinheiro *et al.* 2009).

To account for the hierarchical structure of the data, i.e. individual birds within groups, I used linear mixed effects models (LME) to analyse the relationship between each behavioural parameter and the seed density. The optimum random effects structure for all the behavioural parameters was found to be a random intercept for both the individual bird and the group. There was a consistent violation of homogeneity of variance in the behavioural parameters across the seed densities. One likely source of this heterogeneity of variances is due to the birds having more options in their foraging rate at high densities, i.e. they can forage at their maximum rate or choose to forage more slowly, whereas at low densities they are restricted in their foraging rates by the searching rate. Transformations of the response variable were not sufficient to remove this heterogeneity and, therefore, I allowed for a different variance structure per seed density ('varIdent' in R nlme package).

	Mean observed value	
	Bare soil (± 95% CI)	**Stubble (± 95% CI)**
Habitat structure		
Stubble density (stems m^{-2})	0	70
Behaviour parameters		
$H_t(s)$	0.851 (± 0.04)	-
p (proportion of compatible H_t)	0.521 (± 0.013)	-
v (proportion of time foraging)	0.136 (± 0.013)	-
Search speed (s) ($m\ s^{-1}$)	0.274 (± 0.016)	-
Maximum attack distance (d) (m)	0.293 (± 0.050)	0.233 (± 0.036)
Search rate (a) ($a = 2ds$) ($m^2 s^{-1}$)	0.159	0.129

Table 3.1: The mean observed behavioural parameter values (± 95% confidence intervals) used to parameterise models 1 and 2 to predict the functional responses of grey partridge foraging for wheat seeds in two habitat treatments; bare soil and stubble. For many of these behavioural parameters there was no significant difference between the two treatments and, therefore, these data were combined before analysis (- indicates that the parameter mean was calculated using the combined data and estimate applies to both treatments).

Log10 transformations to the explanatory variable seed density were required for some of the models (feeding rate, H_t, H_x, H_c and search time) where there was a clear violation of linearity. To achieve normal errors, the response variables of H_t, H_x, H_c and search time were Log10 transformed, the frequency of vigilance and duration of vigilance were square-root transformed (+ 0.5 to account for zero values) and the proportion of time spent vigilant was arcsin transformed. The initial fixed factors included in the analysis were seed density, habitat, sex, time-of-day and the interaction between seed density and habitat. Most of these terms were not significantly related to the response variable and, therefore, only significant results are reported. Where habitat did not significantly affect the behavioural parameters (Figs 3.5 and 3.7) the data from both treatments were combined before plotting.

3.4 Results

3.4.1 Behavioural parameters

Feeding rate (Fig. 3.4).

The (log) feeding rate of grey partridge was positively correlated with (log) seed density (LME, $F_{1,261}$= 148.32, $P < 0.0001$), but the presence of crop stubble had no effect (LME, $F_{1,260}$= 0.177, $P = 0.674$).

Handling (Fig. 3.5a-c).

The total handling time (H_t) was negatively correlated with (log) seed density (LME, $F_{1,261}$= 82.406, $P < 0.0001$). The two components of handling time were both negatively correlated with (log) seed density, H_t (LME,$F_{1,261}$= 199.542, P < 0.0001) and H_c (LME, $F_{1,261}$= 20.681, P < 0.0001), but the approach time had a much higher F-value. The presence of crop stubble had no effect on H_t (LME, $F_{1,260}$= 0.706, P = 0.402), H_x (LME, $F_{1,260}$= 0.0692, $P = 0.793$) or H_c (LME, $F_{1,260}$= 2.025 , $P = 0.1559$).

Vigilance (Fig. 3.6a-c).

The proportion of time spent vigilant (v) was negatively correlated with seed density (LME, $F_{1,261}$= 14.901, P < 0.0001), as was the frequency of vigilance bouts (LME, $F_{1,261}$= 19.135, P = <0.0001), but the duration of vigilance bouts was only weakly correlated with seed density (LME, $F_{1,261}$= 4.819, $P = 0.029$). The presence of crop stubble had no effect on v (LME, $F_{1,260}$= 0.02, $P = 0.889$), the frequency of vigilance bouts (LME, $F_{1,260}$= 2.503, $P = 0.115$) or the duration of vigilance bouts (LME, $F_{1,260}$= 0.016 , $P = 0.899$).

Searching (Fig. 3.7).

The maximum attack distance was negatively correlated with seed density (LME, $F_{1,84}$= 9.649, $P = 0.0026$) and was also significantly affected by the presence of crop stubble (LME, $F_{1,84}$= 19.375, $P < 0.0001$). The search time (Fig. 3.7) was negatively correlated with (log) seed density (LME, $F_{1,261}$= 89.768, $P <$ 0.0001), but the searching speed was not affected by seed density at the lowest three densities (LME, $F_{1,89}$= 0.285, $P = 0.5947$). The presence of crop stubble did not affect these two behavioural parameters: search time (LME, $F_{1,260}$= 1.669, P = 0.1975) and searching speed (LME, $F_{1,88}$= 0.0141, $P = 0.9058$).

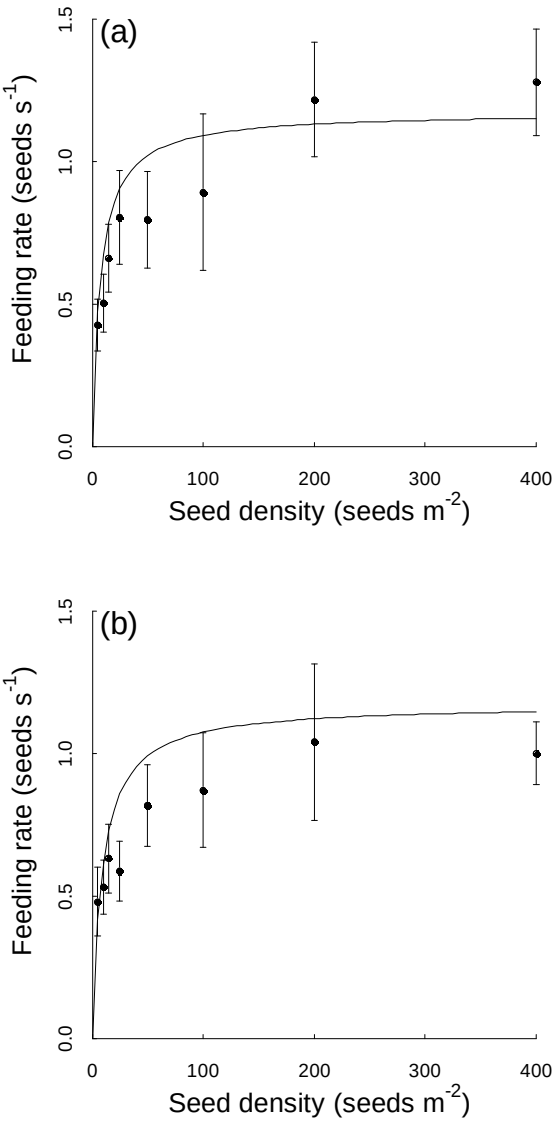

Figure 3.4: The functional responses of grey partridge foraging for wheat seeds in (a) bare soil and (b) stubble treatments. The mean values (± 95% confidence intervals) are given. The curves show the predicted values of feeding rate estimated by models 1 and 2 using the observed values for the behavioural parameters a, H, v and p (see Table 1). The models produce identical estimates of feeding rate when seed density exceeds 3 seeds m^{-2}.

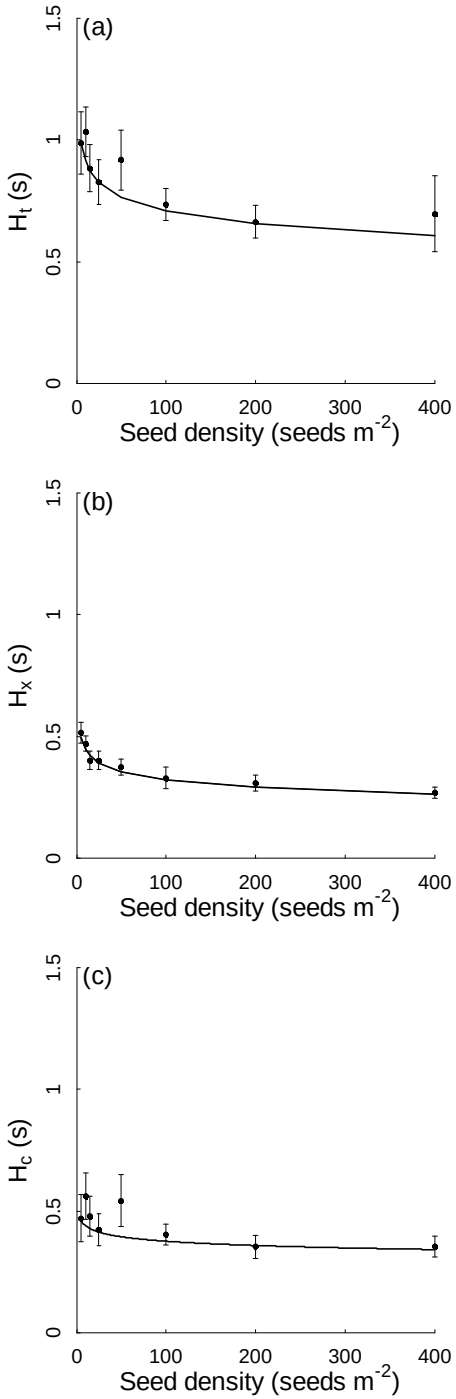

Figure 3.5: The mean observed handling (± 95% confidence intervals) of the grey partridge foraging for wheat seeds; (a) total handling time (H_t) (log(y) = 0.073 - 0.111 • log(x)), (b) incompatible handling time (H_x) (log(y) = 0.204 + 0.144 • log(x)), (c) compatible handling time (H_c)(log(y) = 0.27 + 0.08 • log(x)). The intercept and slope for the associated curves were derived using linear mixed effects models on the transformed data and back transformed before plotting (see methods).

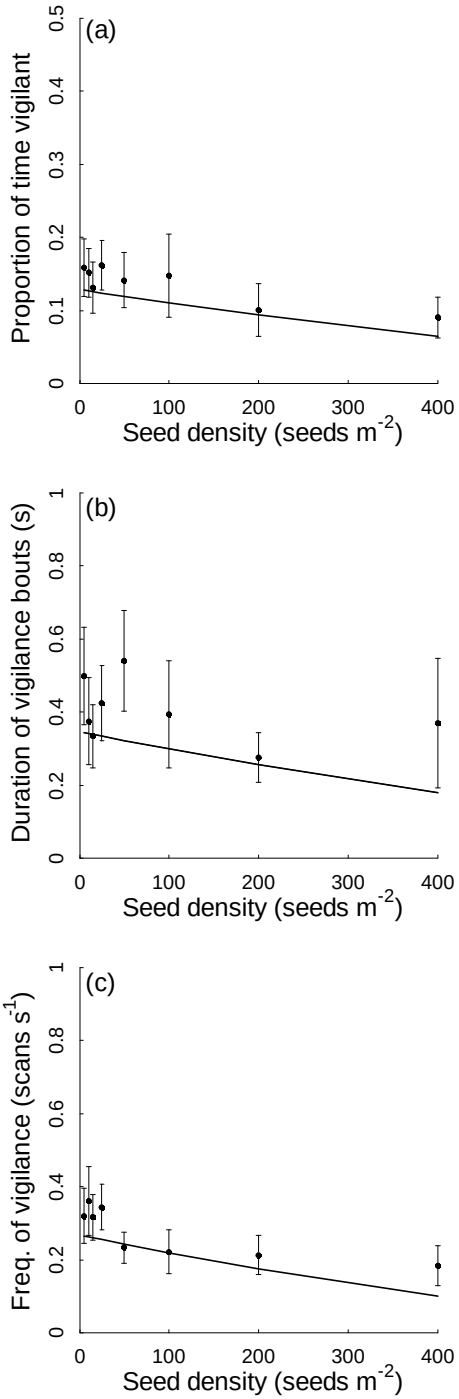

Figure 3.6: The mean observed vigilance parameters (± 95% confidence intervals) of the grey partridge foraging for wheat seeds; , (a) proportion of time spent vigilant (v) (arcsin(y) = 0.367 - 0.0003 • x), (b) duration of vigilance (sqrt(y) = 0.588 – 0.0004 • x), and (c) frequency of vigilance (sqrt(y) = 0.519 – 0.0005 • x). The intercept and slope for the associated curves were derived using linear mixed effects models on the transformed data and back transformed before plotting (see methods).

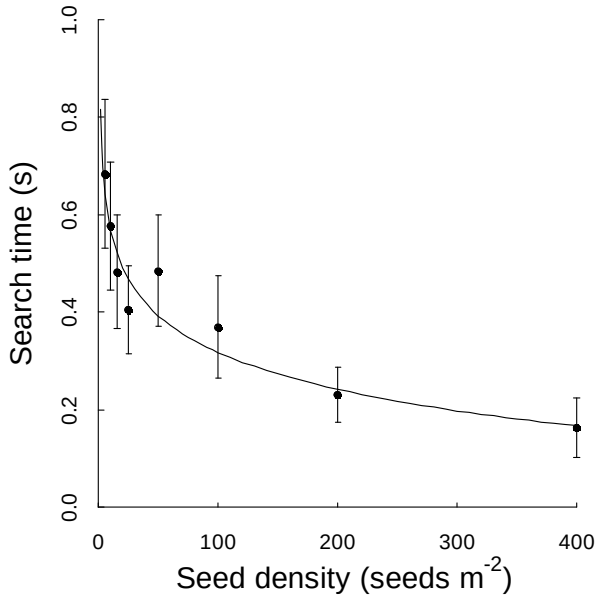

Figure 3.7: The mean observed searching time (± 95% confidence intervals) of grey partridge foraging for wheat seeds (y = 0.817 – 0.25 • log(Density)), defined as the interval between initiation of a search and the beginning of handling. The intercept and slope for the associated curve were derived using linear mixed effects models on the transformed data and back transformed before plotting (see methods).

3.4.2 Predicting the functional response from behavioural parameters

Models 1 and 2 were parameterised using the observed behavioural parameters (Table 3.1) and their predictions of the functional responses were compared. Vigilance was found to only affect the functional response at seed densities < 3 seeds m^{-2} in both treatments, shown by a reduction in the predicted feeding rate, but as this was below the seed densities used in the experiment model 2 has a lower *AIC* and an identical R^2 value to model 1 (see Table 3.2). This suggests that vigilance is starting to affect the functional response, but under these experimental conditions the effect is only slight. To understand how variation in the key behavioural parameters of p and v affects the feeding rate, and how these relationships are themselves affected by prey density, I plotted the feeding rate calculated using model 2 against the proportion of time spent vigilance (v) and the proportion of compatible handling time (p) (Fig. 3.8) at three seed densities (5, 25 and 200 seeds m^2). The values for parameters a and H were the mean observed values

	Model	n	K	AIC_c	$\triangle AIC_c$	A_w	R^2
Bare soil	1	142	2	-281.66		0.891	0.311
	2	142	4	-277.46	4.20	0.109	0.311
Stubble	1	140	2	-288.20		0.891	0.181
	2	140	4	-283.99	4.21	0.109	0.181

Table 3.2: The Akaike Information Criterion (*AIC*) comparing the ability of models 1 and 2 to predict the observed functional response. The Akaike weights (A_w) are used to compare the likelihood of each model relative to the other (Edwards et al 2007).

from the bare soil treatment. These figures indicate that at low seed densities, with even moderate values of p and v, vigilance should begin to affect the functional response of these birds.

Previous studies have shown that the proportion of time spent vigilant in some granivorous bird species can be as high as 60% (Baker *et al.* 2009) and, therefore, it is possible that for these species vigilance will affect the functional response at low prey densities. Setting the values of a and H_t to those reported for chaffinches in Baker *et al.* (2009) and comparing the values of p given $v = 0.578$ or 0.598 (chaffinches, bare soil and stubble treatment, respectively) suggests that vigilance should affect the predicted functional response at all values of $p < 0.916$ or ≤ 1, respectively (see Appendix 1, equation 24), at a seed density of 25 seeds m^{-2}. To test this hypothesis I re-analysed video data for the functional responses of chaffinches in bare soil and stubble treatments, published previously in Baker *et al.* (2009), calculating the value of p. As there was no effect of treatment (bare soil or stubble) on p (lm, $F_{1,205}= 2.114$, $P = 0.148$) I used the mean of the combined data ($p = 0.903$) to calculate the feeding rate using model 2. I found that the feeding rates predicted using model 2 differed from that of model 1 at prey density < 25 seeds m^{-2}, the lowest seed density used in this study, in bare soil treatment and < 42 seeds m^{-2} in the stubble treatment (Fig. 3.9). This indicates that vigilance could affect the predicted functional response at low prey densities in a forager with high vigilance, even when p is high.

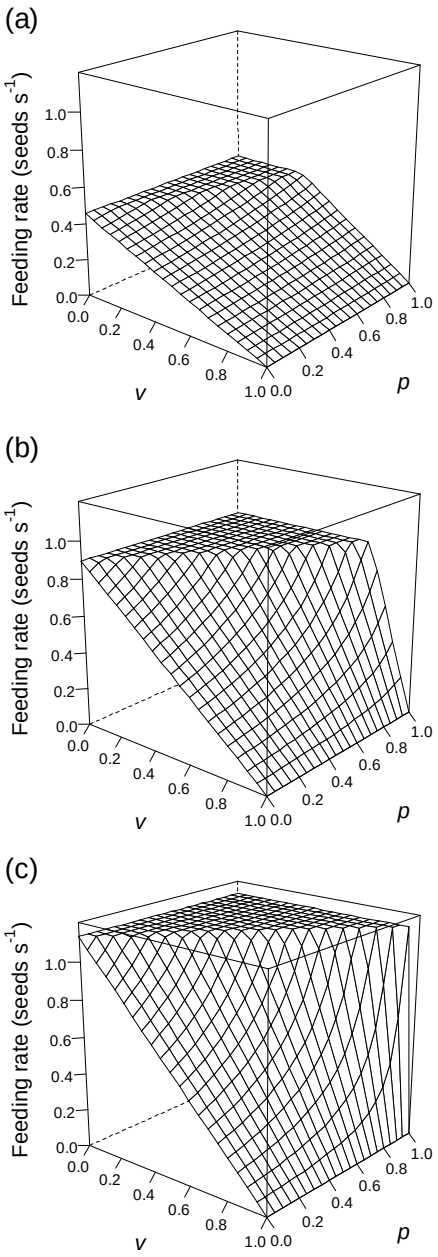

Figure 3.8: Relationships between the proportion of time spent vigilant (v), the proportion of handling time that is compatible with vigilance (p) and feeding rate for grey partridge foraging in the bare soil treatment at; (a) 5 seeds m^{-2}, (b) 25 seeds m^{-2}, and (c) 200 seeds m^{-2}. The plot is calculated using model 2 with the associated parameter values for a and H under the bare soil conditions. The plateaux shows the maximum feeding rate achievable at this seed density under these conditions and the slope indicates a reduction in feeding rate resulting from vigilance. All graphs were produced using the lattice (Deepayan 2010) package in R.

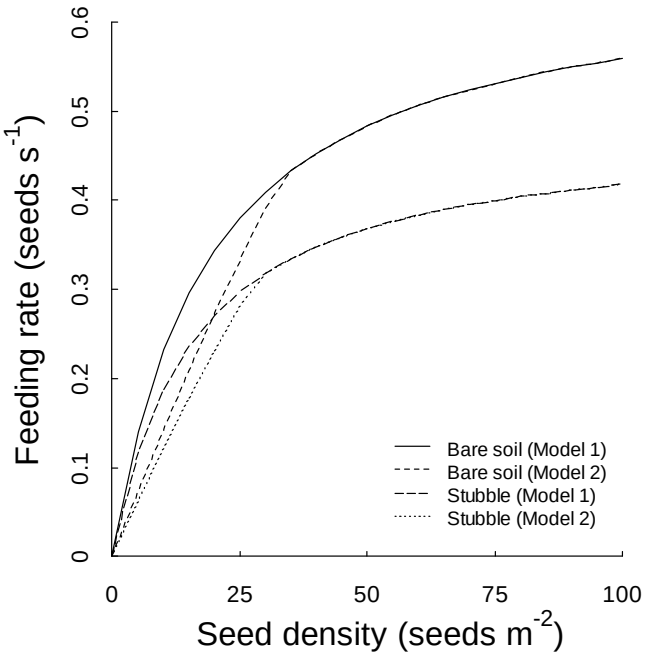

Figure 3.9: The effect of vigilance on the predicted functional response of chaffinches feeding at low seed densities. The parameter values of a, H_t and v for bare soil and stubble treatments were those reported in Baker et al. (2009). The parameter value for p was measured by reanalysis of the original experiment.

3.5 Discussion

I have developed a functional response model (Fig. 3.3.4) that can account for the effect of vigilance on feeding rate when the proportion of time spent vigilant begins to exceed the proportion of handling time that is compatible with vigilance (H_c). When $v = 0$ and $p \geq 0$ the model predicts a response without vigilance (identical to the Holling's disc model). When $v \geq 0$ and $p = 0$ the model predicts a functional response with mutually exclusive vigilance and handling. When $v \geq 0$ and $p = 1$ the model predicts a functional response with completely overlapping vigilance and handling. When parameterised using values for a, H_t, v and p for a granivorous bird, the grey partridge, measured under experimental conditions, the model indicated that vigilance should have an effect on the functional response, but only at very low prey densities (< 3 seeds m^{-2}). However, simulations of the effect of vigilance on feeding rate at different seed densities show how the potential for vigilance to affect feeding rate (i.e. the values of p given v) increases as the proportion of time spent vigilant increases. To test this I parameterised model 2 for a species, the chaffinch, with a higher value of v and found that vigilance reduced feeding rates at higher prey densities and had a larger effect in the stubble treatment.

These results show that when parameterised using observed behavioural parameters vigilance can have an effect on the functional response of a granivorous bird, especially at low prey densities or in obstructed habitats where searching rates are lower. The proportion of time spent vigilant (v) measured for grey partridges in this study was lower than expected (Watson *et al.* 2007), most likely caused by using intensively reared captive birds (Beani & Dessi-Fulgheri 1998), and consequently this mitigated the impact of the low H_c. Assuming that the other parameters will remain unchanged, the value of v (i.e. v = ~0.4) observed in wild grey partridges (Watson *et al.* 2007) would increase the effect of vigilance on the functional response. However, extrapolating these conclusions from captive grey partridge to wild birds is not productive given the uncertainty about the values for the remaining behavioural parameters in wild birds. The effect of vigilance on the functional response of wild chaffinches (Fig. 3.9) suggests that vigilance can be an important limiting factor in the functional response of wild birds and, therefore, is likely to impact on their foraging behaviour when prey resources are low. The presence of crop stubble was predicted to increase the effect of vigilance on

the functional response by reducing the searching rate. Although, this was found to have occurred in the chaffinch study no effect was found with the grey partridges, suggesting that the stubble did not sufficiently reduce the searching rate for an effect to be observed.

The impact of vigilance on a forager may not always manifest itself in reduced feeding rates as individuals could adjust other behaviours, i.e. through patch choice or joining a larger groups of foragers, in order to maximise their feeding rates and minimise their predation risk (Jones, Krebs & Whittingham 2006; Whittingham & Evans 2004; Beauchamp 2009). Butler *et al.* (2005b) showed that switching to a more obstructed patch only occurred once the ratio of the prey densities between the two patches had exceeded a threshold, when the benefit of foraging in a more risky environment had exceeded the risk, i.e. increased feeding rate at the expense of vigilance. In experiments with no option of patch switching, as prey density decreases, any effect of vigilance on foraging behaviour is likely to be displayed through a reduction in feeding rate, as reported here. I found no significant difference between the vigilance parameters in the two treatments; however, the stubble was primarily used to provide a physical obstruction to reduce the searching rate and, therefore, may not have been high enough to change the vigilance behaviour.

The relationship between prey density and v found here shows that the birds were spending more time vigilant at low prey densities, which is contrary to some previous studies on granivorous birds (Baker *et al.* 2009; Smart *et al.* 2008), but predicted when foragers are time constrained (Beauchamp 2009). Although it is possible that the birds perceive the limited time available for foraging on the platform as a time constraint this is uncertain as they were accustomed to receiving *ad libitum* food outside of the experimental period. A more likely explanation is that the higher proportion of time spent vigilant at low densities is a consequence of the longer observed compatible handling times at these densities. These similar, but non-linear, negative correlations were found for all the handling time parameters and might have been missed in other studies that used higher prey densities. The negative correlation between seed density and the H_x component of handling time was expected as this component includes the time taken to approach the target prey item, which is negatively correlated with density. However, the negative correlation between seed density and H_c was not expected as I anticipated that the time take to process a prey item would be independent of its density. It is possible

that prey is processed more carefully when it is less abundant as the scarcity of the resource makes its full exploitation more important. Furthermore, the birds could use some of this handling time to scan for other prey items. However, the corresponding increase in vigilance suggests the birds occupy this additional handling time with further vigilance.

Both models were able to predict the functional responses from observed behavioural parameters very successfully, and, despite the low R^2 values, the models capture both the shape of the observed response and the asymptote. The low R^2 values are a consequence of the large variability in the observed feeding rate, which is to be expected in a behavioural study, but are similar to those achieved for corn bunting foraging on wheat (Smart *et al.* 2008). From this study it is not possible to determine how well model 2 captures the shape of the functional response once vigilance starts to limit the feeding rate as this point was always reached at or below the prey densities measured in these experiments. This could be studied experimentally if the values of v and p could be manipulated so that the effect of vigilance could be observed at higher densities. Suggestions for achieving this might include: matching the background colour to the prey colour to make the prey less conspicuous; using uneven surfaces or a courser grained substrate; using larger foraging areas with lower prey densities; using smaller prey items; and using dummy predators or predator calls.

Although model 2 was derived and tested around the foraging behaviour of granivorous birds its potential should be considered for all species that forage for discrete immobile prey items and have short handling times relative to the time spent vigilant. The assumptions of the model should not limit its utility to any particular taxonomic group, but more importantly the foraging behaviour of the subject should be considered before applying the model. Examples might include: grey squirrels *Sciurus carolinensis* foraging for seeds and nuts (Makowska & Kramer 2007) and samango monkeys *Cercopithecus mitis erythrarchus* foraging for fruit (Cowlishaw *et al.* 2004). The functional response model developed by Fortin *et al.* (2004) to describe the foraging cost of vigilance in mammalian grazers/browsers has broad similarities to model 2 presented here. However, functional response models for these forager types might not be directly applicable to granivorous foragers due to the behavioural adaptations of foragers to these prey resources, i.e. the possibility of multiple bites from one resource (Spalinger & Hobbs 1992) and of cropping further bites whilst still handling (Fortin *et al.*

2004). These extra complexities mean that functional response models derived for grazers/browsers often include parameters that are unnecessary when applied to granivorous foragers (Fortin *et al.* 2004; Hobbs *et al.* 2003; Spalinger & Hobbs 1992).

Here I have shown that vigilance can affect the predicted functional response of a granivorous bird and have derived a new functional response model that can predict when such effects should be observed. Understanding the effects of vigilance on the functional response will be important if we are to fully understand the foraging decisions and patterns that are observed in the wild. For mechanistic models that use functional responses to link population level demographic processes to environmental parameters (Butler *et al.* 2010) the incorporation of vigilance may have significant consequences for predicting the distribution of foragers and patterns of resource depletion. Perceived differences in predation risk between patches is likely to cause some patches to be avoided when prey is abundant resulting in an uneven depletion of resource across the landscape. Some patches will maintain higher densities of prey that can be exploited, at higher predation risk, when resources elsewhere are exhausted. This model will provide a useful tool for exploring the implications of vigilance on larger scale ecological processes and for developing mechanistic models for conservation management.

3.6 References

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Supplementary material

Additional supporting information may be found in the Appendix (Page 224- 228)

Appendix 1. Derivation of functional response with mutually exclusive searching, and partially overlapping handling and vigilance (model 2)

Chapter 4

Are the costs of routine vigilance avoided by granivorous foragers?

A version of this chapter is published as the following:

Baker, D.J., Stillman, R.A., Smart, S.M., Bullock, J.M. & Norris, K.J. (In press) Are the costs of routine vigilance avoided by granivorous foragers? Functional Ecology.

4.1 Abstract

1. Routine vigilance is an important component of foraging for many species and can occupy a large proportion of this time. Vigilance can conflict with some aspects of foraging (i.e. searching) and, consequently, has the potential to reduce feeding rates by interrupting foraging behaviours. However, for animals that handle food in an upright posture vigilance can be compatible with this portion of handling and, therefore, any vigilance during this time will incur minimal time-costs to foraging.

2. Several functional response models that incorporate vigilance have assumed that, (i) vigilance preferentially occurs during compatible portions of a foraging routine where no costs are incurred; and (ii) vigilance can be treated as a single discrete block of time related in frequency to the feeding rate, i.e. one vigilance scan per feeding event.

3. To determine whether these assumption are appropriate we measured the vigilance behaviour of four species of granivorous bird, yellowhammer,

tree sparrow, linnet and grey partridge, and assessed the quantity of vigilance compared to compatible handling time, the relationship between scan rate and feeding rate and the distribution of vigilance during compatible and non-compatible portions of foraging.

4. The results show that there was frequently enough compatible handling time to accommodate routine vigilance, yet a high proportion of vigilance occurred during non-compatible components of foraging, thus incurring a time-cost. The frequency of vigilance bouts was higher than the feeding rate for three species and, therefore, routine vigilance was not just a by-product of the feeding rate (i.e. one scan per peck). Frequent head-down searching behaviour was recorded during handling suggesting that searching is still a prominent component of foraging even when prey is superabundant.

5. We have shown that the assumptions of previous functional response models might underestimate the effects of vigilance on feeding rate by overestimating the proportion of compatible handling devoted to vigilance. Future functional response models must account for this distribution of vigilance between compatible and non-compatible behavioural states. We derive an example of such a model; however, more experimental research will be needed before we understand the factors that influence the distribution of vigilance.

4.2 Introduction

Vigilance is a major component of foraging for many animals, whether aimed at detecting approaching predators or for surveillance of nearby conspecifics (Beauchamp 2009; Favreau, Goldizen & Pays 2010). Whilst vigilance is often induced by external stimuli (Rainey, Zuberbuhler & Slater 2004; Bell *et al.* 2009), much time is devoted to routine vigilance (Blanchard & Fritz 2007). Routine vigilance can be adjusted towards the potential risk (Guillemain, Duncan & Fritz 2001; Devereux *et al.* 2006; Jones, Krebs & Whittingham 2007) or to accommodate incompatible behaviours such as searching (Lawrence 1985) or scrounging (Coolen & Giraldeau 2003). Given the importance of routine vigilance for a foraging animal it might be assumed to have a limiting effect on feeding rate (Elgar

1989; Beauchamp & Livoreli 1997; Fritz, Guillemain & Durant 2002). However, whilst the assumption that vigilance will affect feeding rate seems intuitive there are often opportunities to engage in vigilance such that time-costs are reduced or avoided (Fortin, Boyce & Merrill 2004a; Fortin *et al.* 2004b; Baker *et al*. 2010). For instance, species that handle food in a head-up posture can use the head-up component of handling for vigilance without incurring significant time costs (Lima, Zollner & Bednekoff 1999; Cowlishaw *et al.* 2004). In addition, for some species searching and vigilance may be mutually compatible when prey is detected from a distance. Illius & Fitzgibbon (1994) derived a simple model to show the circumstances under which vigilance costs could be reduced or avoided by grazing herbivores. They found greater food availability allowed higher levels of 'cost-free' vigilance, i.e. higher biomass cropped per bite and less searching time, and also showed that larger animals were more susceptible to the cost of vigilance due to an increased sensitivity to low food densities. Similarly, Cowlishaw *et al.* (2004) showed that when the ratio of compatible prey handling (i.e. head-up) to searching time is high (i.e. at high prey densities) a forager is able to perform routine vigilance without a reduction in feeding rate.

Several functional response models, i.e. those that predict feeding rate as a function of prey density, have incorporated the effects of routine vigilance and its interaction with handling time. Fortin *et al.* (2004b) derived a functional response model that demonstrated how 'spare time' can result from handling limitations when the encounter rate is faster than the rate of handling and that this 'spare time' could be allocated to vigilance. Here it was shown that vigilance often reduced the intake rate of grazing herbivores even when there was adequate time for cost-free vigilance during handling. Several functional response models have explicitly included vigilance as a parameter and have allowed the interaction between vigilance, handling and searching to vary in several ways (Smart, Stillman & Norris 2008; Baker *et al.* 2010). Smart *et al.* (2008) allowed the proportion of time spent vigilant to overlap with the total time spent handling and found that vigilance had no effect on the predicted feeding rate. Baker *et al.* (2010) divided handling time into two components, the head-down approach component that is incompatible with vigilance (H_x) and a head-up processing component that is compatible with vigilance (H_c). A functional response model was derived that allows vigilance to interact with only the H_c portion of prey handling and it was found that when allowing such an interaction vigilance affected the predicted

feeding rate when prey density was very low, i.e. ratio of compatible handling to searching was high (Cowlishaw *et al.* 2004). Thus, the incorporation of vigilance into the functional response model has not predicted the large decreases in feeding rate that might be anticipated. This raises two questions: (i) does vigilance have a limiting effect on feeding rate in these species? And (ii) do these models realistically represent vigilance and its effect on feeding rate?

Such functional response models that have explicitly incorporated routine vigilance have treated vigilance as a discrete block of time (i.e. the proportion of time vigilant) (models 4 & 5 (Smart *et al.* 2008) and model 2 (Baker *et al.* 2010)), assuming that the effect of vigilance on feeding rate depends on whether the proportion of time vigilant is greater than the proportion of compatible handling time. Thus, two assumptions are made regarding the properties of vigilance: (i) that vigilance preferentially occurs during compatible portions of a foraging bout where no costs are incurred; and (ii) that vigilance can be treated as a single discrete block of time related in frequency to the feeding rate, i.e. one vigilance scan per prey consumed. Whether such simplifying assumptions are appropriate for these functional response models is questionable especially when considering the assumptions of classic vigilance models, i.e. random initiation of vigilance scans (Pulliam 1973; Bednekoff & Lima 1998). If the assumptions of the classic vigilance models are correct then vigilance scans could be initiated during any portion of a foraging bout with equal probability and, therefore, vigilance is likely to have a greater impact on the functional response than predicted by these functional response models. However, there are apparent differences between these classic vigilance models and the foraging behaviour of many granivorous foragers, most notably the tendency to handle prey in an upright posture. Thus, where the vigilance models assume head-down foraging interrupted by randomly induced head-up vigilance bouts these granivorous foragers tend to move sequentially into a head-up posture after making contact with a seed (i.e. non-random).

There is now considerable evidence to show that the assumptions of classic vigilance models considerably over simplify vigilance behaviour, especially in regards to the randomness of scan initiations (Bednekoff & Lima 1998; Beauchamp 2006; Pays *et al.* 2010) and the synchronisation of vigilance scans between conspecifics (Pays *et al.* 2007a; Pays *et al.* 2007b). This might suggest that the timing of vigilance scans and their duration is flexible enough to accommodate vigilance where the costs are lowest. Carrying out vigilance scans only during

compatible portions of a foraging bout might not provide the optimum strategy for detecting an approaching predator and therefore a trade-off is likely between reducing the costs of routine vigilance and maximising the feeding rate. Frequent short vigilance scans have been shown to increase the probability of detecting an approaching predator (Cresswell *et al.* 2003; Whittingham *et al.* 2004), but the proportion of time spent vigilant and the mean scan duration do not correlate strongly with predator detection. An increased scan rate appears to correlate with a higher instantaneous intake rate (Gluck 1987; Fritz *et al.* 2002; Whittingham *et al.* 2004) although this is probably a consequence of higher foraging efficiency and not due to the vigilance frequency *per se*. Thus, the optimum strategy for detecting a predator might be frequent scans of short duration and this might conflict with the frequency and pattern of compatible handling time. Whether vigilance is an important and necessary component in functional response models is of interest because vigilance adds significant complexity to the functional response model. However, if functional response models can be developed that accurately incorporate the effects of vigilance then these models will be have great application to applied conservation issues where the functional response can be used to link resource density to feeding rate and ultimately individual survival (Stephens *et al.* 2003; Goss-Custard *et al.* 2006).

Here we aim to assess the assumptions of previous functional response models, specifically the interaction between vigilance and compatible handling time and the temporal distribution of vigilance throughout the foraging bout. We test: (i) the relationship between three measures of vigilance and food density; (ii) whether the amount of time spent vigilant for each peck exceeds the amount of compatible handling time (H_c) and, therefore, whether a time-cost is incurred; (iii) the relationship between the frequency of vigilance scans and the feeding rate to determine whether vigilance scans are a consequence of the feeding rate; and (iv) compare the proportion of time spent vigilant during H_c and non-H_c foraging time and, therefore, whether the assumption that vigilance occurs when its costs are minimised is correct. To address these questions we measured the functional response and the associated behavioural parameters (handling time (H_t (total = H_c + H_x), H_c & H_x), proportion of time vigilant, duration of vigilance scans, frequency of vigilance scans, vigilance during Hc, vigilance during non-Hc) of three species of European granivorous farmland bird (Fig. 4.1), yellowhammer *Emberiza citronella* L, tree sparrow *Passer montanus* L, and linnet

Figure 4.1: Photographs of two of the species used in this study, from left to right: yellowhammer *Emberiza citronella* L (photograph by David Baker); grey partridge *Perdix perdix* L (photograph by Peter Thompson). The remaining two species used here have similar physical characteristics to the yellowhammer.

Carduelis cannabina L. Additionally, we re-examine the data for grey partridge *Perdix perdix* L presented in Baker *et al.* (2010) with the expectation that the majority of vigilance here will occur during the compatible components of foraging as little effect of vigilance on the functional response was predicted by the functional response model in this study. We find that the data from these species do not entirely support the assumptions of previous functional response models incorporating vigilance, and so derive two new functional response models with more realistic assumptions. We discuss the implications of these results for functional response models and especially those that incorporate vigilance.

4.3 Methods

4.3.1 Handling time and vigilance: definitions

Holling (1966) defined handling time as a function of the time spent: (i) pursuing and subduing each prey item; (ii) eating each prey item; and (iii) in 'digestive

pause'. Because we will be measuring the foraging behaviour over a short time interval and, therefore, the birds are not likely to be satiated during that time only the first two components of Holling's definition are appropriate. In this study the first component of handling is termed H_x and can be considered the attack component (the x indicating incompatibility with vigilance). H_x is included as a part of handling because once an attack has begun the forager's focus is on only a single prey item and thus it can be recorded as the time taken to capture a single prey. The second component is termed H_c and represents the processing and ingestion of each prey item (the c indicating compatibility with vigilance).

In this study we have tried to quantify the proportion of time a forager spends vigilant in order to predict the impact of this behaviour on the functional response. In order to do this we chose to define routine vigilance behaviour as the time spent with the head in an upright posture with the bill parallel to the ground or at a greater angle. However, this definition is largely taken for practical reasons because it is possible to observe and quantify this behaviour during video analysis. Whilst this posture is likely to signal routine vigilance, several studies have shown that predator detection still occurs in head-down postures, a position that has been defined here as non-vigilant. For example, Lima *et al.* (1999) showed that dark-eyed juncos *Junco hyemalis* L were still able to detect a simulated predator with their head-down, although over a shorter distance. Bednekoff & Lima (2005) found that these birds preferred to forage in a habitat where their visual field was not obstructed when in a head-down position. However, it is clear that head-up vigilance is the optimum posture for detecting predators as foragers tend to increase the amount of head-up scanning in response to higher predation risk or reduced detection potential (Elgar 1989; Whittingham *et al.* 2004). Therefore, head-up time is probably the best indicator of the perceived threat and is a good metric of the time-costs incurred by engaging in routine vigilance. The targets of routine vigilance might be either predators or conspecifics and it is possible that these different targets could induce different patterns of vigilance. However, granivorous foragers tend to have short handling times that offer little opportunity for kleptoparasitism or scrounging and thus the benefits of monitoring conspecifics are probably not as important as for many group foraging species (i.e. shorebirds (Stillman, Goss-Custard & Caldow 1997)).

4.3.2 Functional response data

Here I used data from three separate functional responses of three different granivorous bird species, yellowhammer, tree sparrow and linnet feeding on wheat, millet and rapeseed, respectively. In addition, I re-examined one functional response data set presented in Baker *et al.* (2010) for grey partridges foraging for wheat seeds on bare soil, extracting additional parameters where necessary.

4.3.3 Behavioural experiment

4.3.3.1 Functional response and vigilance experiments

The functional response experiments were conducted as follows: the linnet experiment was conducted at Woodborough Hill Farm, Wiltshire, England between the 1st and 3rd February 2006: the tree sparrow experiment was conducted at Easton Farm, Wiltshire, England between the 5th and 7th April 2006; and the yellowhammer experiment was conducted at Stanton St Bernard Farm Wiltshire, England between the 22nd March 2006 and the 6th April 2006. The protocol of these experiments closely follows that of Smart *et al.* (2008) and, to a lesser extent, Baker, Stillman & Bullock (2009) but will be briefly summarised here. The functional response experiments were conducted on plywood and concrete feeding platforms measuring 1 m x 1.5 m and dyed and textured to mimic the surrounding soil. The birds were presented with different densities of scattered seeds (125, 250, 500, 1000, 2000, 3000, 4000 seeds m^{-2}) in a random order and three replicates were carried out for each density. The experiments were conducted between 09:00 and 15:00 h and each replicate was filmed using a Canon 3CCD XL1 video camera (www.canon.co.uk) for at least 15 minutes from a distance of approximately 30 m, filming along the length of the platform. Outside the periods of the experiment the platforms were covered and seed scattered on top to keep the birds attracted to the area.

4.3.3.2 Analysis of functional response & behavioural experiments

The video footage was downloaded onto a PC and analysed using a purpose-built event recorder. During the analysis we were careful to analyse sequences where large groups of birds were foraging on the feeding platforms simultaneously to avoid including the same individual more than once. These sequences were rela-

tively easy to find here as the seed densities used were high and the birds quickly flocked to the platform. Where there were fewer than 15 birds foraging simultaneously on the platform all the birds that engaged in a foraging sequence of >5 pecks (uninterrupted by obviously induced vigilance bouts) were recorded. Where >15 birds were feeding simultaneously on the feeding platform focal individuals were randomly selected from those individuals that engaged in foraging sequences >5 pecks on a previously unused portion of the platform (to exclude significant depletion effects). The feeding rate was measured from the frame before the bird made contact with the first seed until the frame before the bird made contact with the last seed for a minimum of five pecks. Because we are interested in measuring the instantaneous feeding rate, which excludes the digestive processes associated with the long-term feeding rate, sequences were terminated after a maximum of eight pecks.

Vigilance was defined as time spent with the head positioned so that the bill is parallel to the ground, or at a greater angle. The proportion of time spent vigilance was defined as the proportion of the recorded foraging bout in which the bird was vigilant. The duration of vigilance bouts is the mean duration of all vigilance bouts within a single foraging sequence. The frequency of vigilance is the number of times the head was raised into a vigilant position during the foraging sequence. The time spent vigilance per peck was calculated from the total amount of vigilance during a foraging sequence divided by the number of pecks. The number of individuals feeding within the immediate vicinity of the platform (an area of ~2 m^2) was recorded at each vigilance scan. This represented the core of the flock which can become defuse at the edges and is therefore difficult to define absolutely. The attack portion of handling time (H_x) was measured from the frame at which the bird began moving decisively towards the target prey until the frame before contact was made with the prey item.

The compatible portion of handling time (H_c) was measured from the frame at which the bird made contact with the seed until the frame at which the bird stopped manipulating the seed in its bill. This distinction was chosen because it marks the transition to a state in which the head can be raised without losing the functionality of processing. Once the seed has been seized vigilance can occur without affecting handling whereas prior to this moment any vigilance will decrease the feeding rate. The amount of vigilance that occurred during Hc was recorded and subtracted from the total amount of vigilance during the foraging

sequence, which yielded the amount of vigilance during non-compatible foraging activities: these were converted into proportions.

Here we define the end of H_c based on bill movement and consequently assume that handling subsequent to the cessation of bill movement is negligible (i.e. swallowing). This assumption is often made in handling time studies and here we make this assumption based on several lines of evidence. Firstly, using additional data (DJB unpublished) of yellowhammers feeding on millet seeds (length ~ 3 mm) we found that the mean time between the end of H_c (cessation of bill movement) and the beginning of the next H_x (attack phase) was not significantly different between yellowhammers feeding on wheat (length ~ 6 mm) or millet (t-test, t_{98}= -0.776, P = 0.440). If further processing occurs after manipulation in the bill and before the beginning of the next attack we would expect this to take longer with the substantially larger wheat seeds and this suggests that further processing time is negligible. Furthermore, Zweers (1982) showed using live x-ray imaging that the time taken to pass food into the pharyngeal cavity was very rapid in pigeons *Columba livia* L and that multiple food items could be consumed before a bottleneck was reached in the pharynx.

4.3.4 Statistical analysis

To compare the proportion of time vigilant, duration of vigilance and frequency of vigilance to food density we fitted linear mixed-models. The most likely model based on Akaike Information Criterion (AIC) was a random intercept model with trial as a random factor. For the grey partridge experiment, where each individual bird was individually identifiable, Bird_ID was included as a random factor. Group size was initially included as an explanatory variable in each model and removed when not significant. The residuals were checked for normality and heteroscedacity to determine whether a transformation was required. Only the duration of vigilance showed a non-normal distribution of the residuals and this was corrected with a log transformation of this response variable (for all three species). The time spent vigilant per peck and H_c per peck were compared by fitting linear mixed-effects model, as above, testing the significance of the intercept = 0 and slope = 1. An identical approach was taken for the relationship between the frequency of vigilance bouts and the feeding rate. The amount of vigilance during H_c and non-H_c was compared using a paired t-test for each species separately. All statistical analysis was completed using R 2.10.0. (R Development

Core Team 2009) and the nlme package (Pinheiro *et al.* 2009).

4.4 Results

4.4.1 Food density and vigilance

Feeding rate for each of the three species showed no significant correlation with seed density: yellowhammer (b = 0.00001, t_{12} = 0.264, P = 0.797); tree sparrow (b = 0.000001, t_{13}= 0.456, P = 0.656); linnet (b = -0.00002, t_{12} = -0.528, P = 0.607), where b = the slope of the regression model. The proportion of time spent vigilant was not correlated with seed density for yellowhammer (Fig. 4.2a) (b = 0.0000003, t_{12} = -0.022, P = 0.983), tree sparrow (Fig. 4.2b) (b = 0.00002, t_{13} = 1.09, P = 0.296) and linnet (Fig. 4.2c) (b = 0.00003, t_{12} = 1.178, P = 0.262). There was no effect of seed density on the frequency of vigilance (yellowhammer (Fig. 4.3a) (b = 0.00003, t_{12} = 1.182, P = 0.26); tree sparrow (Fig. 4.3b) (b = 0.00003, t_{13} = 1.248, P = 0.234); linnet (Fig. 4.3c) (b = 0.00004, t_{12} = 1.042, P = 0.318)) or the natural log transformed duration of vigilance (yellowhammer (Fig. 4.4a) (b = -0.00006, t_{12} = -1.422, P = 0.18); tree sparrow (Fig. 4.4b) (b = 0.00002, t_{13} = 0.707, P = 0.492); linnet (Fig. 4.4c) (b = 0.00001, t_{12} = 0.471, P = 0.646)). Table 4.1 shows the mean and 95% confidence intervals for the three measurements of vigilance for all species.

4.4.2 Can routine vigilance be accommodated during H_c?

I compared the mean time spent vigilant (s) for each peck during an individual foraging sequence with the mean H_c (s) for the same foraging sequence to determine whether routine vigilance could be accommodated into the compatible portion of handling (H_c) subsequent to each peck. Table 4.2 shows the results for the linear regression of time spent vigilant against H_c testing for the intercept = 0 and the slope = 1. For yellowhammer (Fig. 4.5a) the intercept was significantly different from zero suggesting that the time spent vigilant was consistently greater than the amount of H_c. Both tree sparrow (Fig. 4.5b) and grey partridge (Fig. 4.5d) spent significantly less time vigilant per peck than the amount of H_c: for grey partridge these results are consistent with Baker *et al.* (2010). The linnets (Fig. 4.5c) spent more time vigilant per peck than H_c when the duration of H_c was short, however, this difference decreased as the amount of H_c per peck

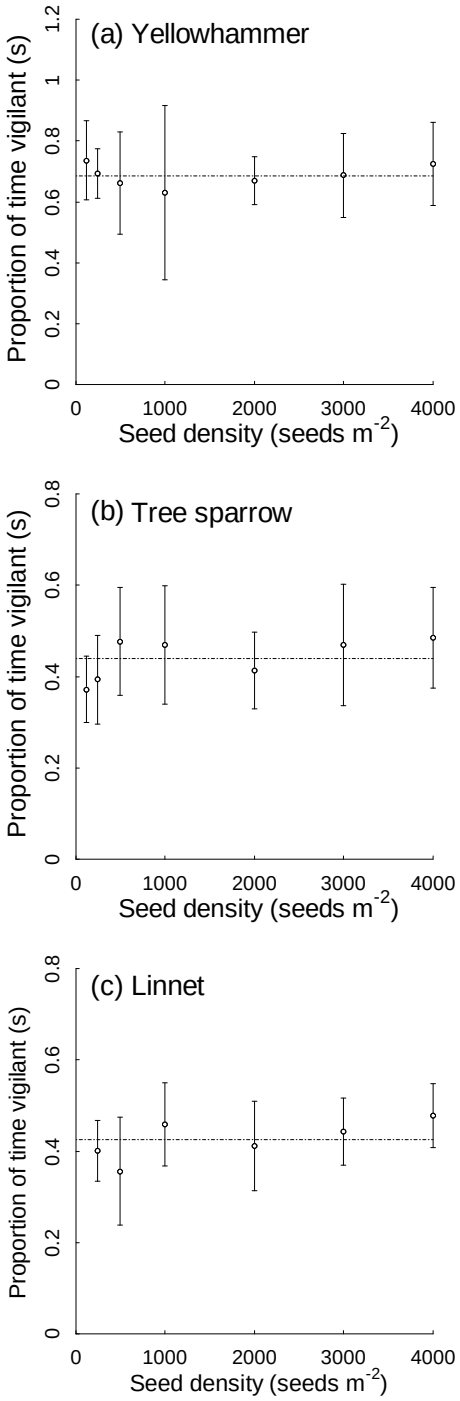

Figure 4.2: The relationship between the proportion of time spent vigilant and food density for: (a) yellowhammer (wheat); (b) tree sparrow (millet); and (c) linnet (rapeseed). The mean at each food density is shown with the associated 95% confidence intervals. The dashed (- - -) line shows the mean for the whole data set where no correlation was present.

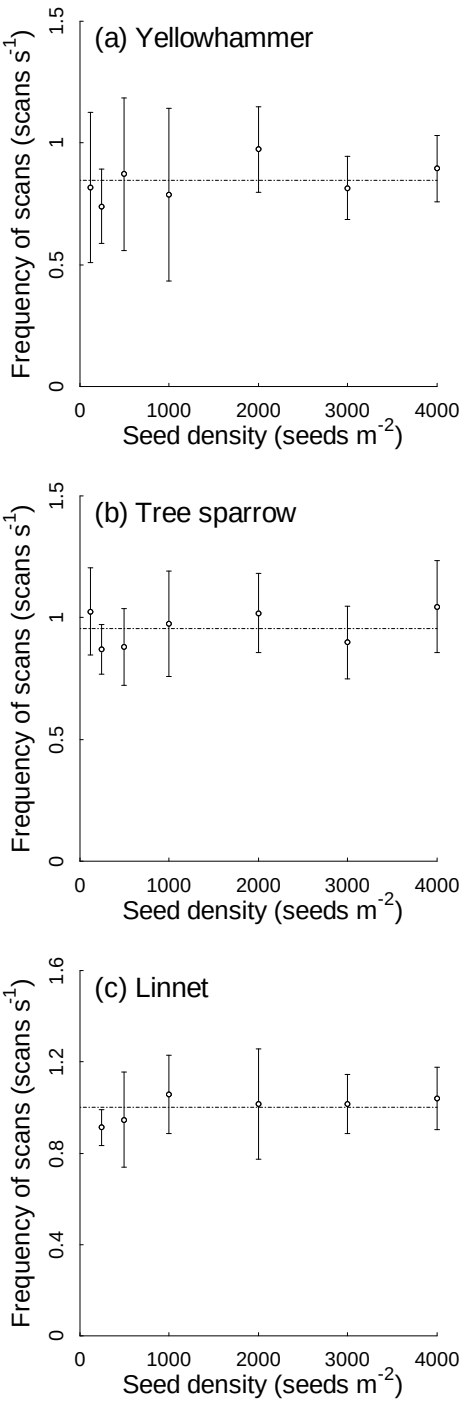

Figure 4.3: The relationship between the frequency of vigilance scans (scans s-1) and food density for: (a) yellowhammer (wheat); (b) tree sparrow (millet); and (c) linnet (rapeseed). The mean at each food density is shown with the associated 95% confidence intervals. The dashed (- - -) line shows the mean for the whole data set where no correlation was present.

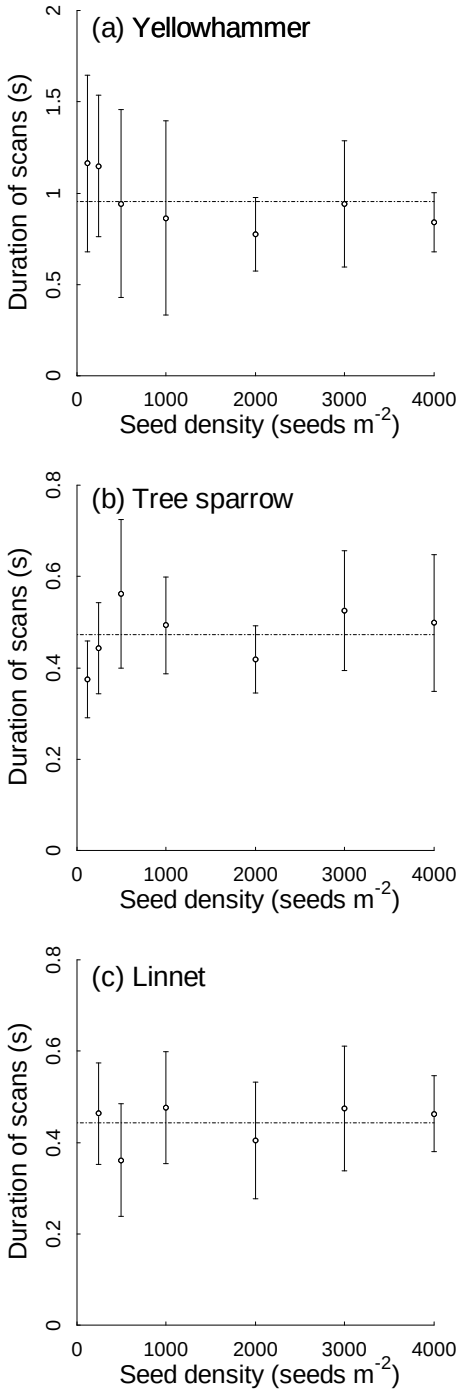

Figure 4.4: The relationship between the duration of vigilance scans (s) and food density for: (a) yellowhammer (wheat); (b) tree sparrow (millet); and (c) linnet (rapeseed). The mean at each food density is shown with the associated 95% confidence intervals. The dashed (- - -) line shows the mean for the whole data set where no correlation was present.

Vigilance behaviour	Species	Mean	95% CI
Proportion time vigilant	Yellowhammer	0.699	± 0.045
	Tree sparrow	0.438	± 0.037
	Linnet	0.452	± 0.030
Frequency of vigilance scans	Yellowhammer	0.851	± 0.073
	Tree sparrow	0.957	± 0.057
	Linnet	1.036	± 0.053
Duration of vigilance scans	Yellowhammer	0.965	± 0.134
	Tree sparrow	0.473	± 0.043
	Linnet	0.465	± 0.042

Table 4.1: The mean (± 95% confidence intervals) estimate of three measures of vigilance for each of the three species of granivorous passerine included in this study. There was no significant effect of prey density on each of these behavioural parameters and therefore this data was pooled to estimate the overall mean.

increased until vigilance was shorter than H_c for H_c values over one second per peck.

4.4.3 How is routine vigilance distributed during foraging?

Although it often appears that time spent vigilant is approximately equal to or less than the H_c portion of handling it does not necessarily follow that this vigilance is distributed entirely within H_c. Figure 4.6 and Table 4.3 shows that the frequency of vigilance scans are often higher than the feeding rate and therefore multiple vigilance scans occur during an average feeding event (i.e. a single peck). For yellowhammer, tree sparrow and linnet the frequency of vigilance scans tends to be greater than the feeding rate, although for the latter two this effect diminishes as the feeding rate increases. For grey partridge the frequency of vigilance is consistently lower than the feeding rate suggesting multiple pecks between vigilance scans. Here the frequency of scans appears to be consistent regardless of the feeding rate.

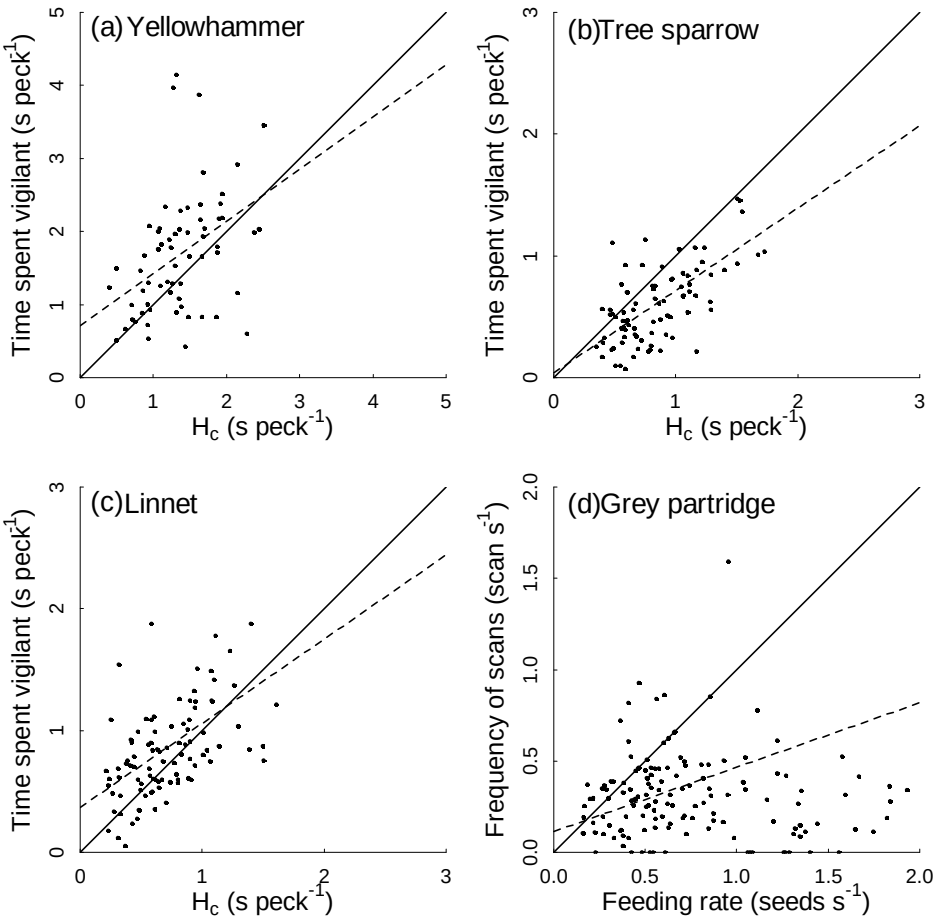

Figure 4.5: The mean time spent vigilant per peck (s) against the mean compatible handling time (H_c) per peck (s) for: (a) yellowhammer (wheat); (b) tree sparrow (millet); (c) linnet (rapeseed); and (d) grey partridge (wheat). The solid (**—**) line is the 1:1 line and the dashed (- - -) line is the linear trend for this data.

Species		Coefficient	Std error	df	*t*-value	*P*
Yellowhammer	Intercept = 0	0.718	0.288	49	2.950	0.016
	Slope = 1	0.713	0.196	49	-1.470	0.148
Tree sparrow	Intercept = 0	0.040	0.077	67	0.518	0.606
	Slope = 1	0.676	0.085	67	-3.829	<0.001
Linnet	Intercept = 0	0.372	0.093	78	4.013	<0.001
	Slope = 1	0.691	0.119	78	-2.605	0.011
Grey partridge	Intercept = 0	0.115	0.051	120	2.269	0.025
	Slope = 1	0.353	0.088	120	-29.011	<0.001

Table 4.2: The linear regression coefficients and significance tests of the intercept = 0 and the slope = 1 for the mean time spent vigilant and the mean compatible handling time (H_c). There was no effect of food density on vigilance across the densities used in this analysis so the data was pooled.

Species		Coefficient	Std error	df	*t*-value	*P*
Yellowhammer	Intercept = 0	0.399	0.065	49	6.150	<0.001
	Slope = 1	0.949	0.117	49	-0.435	0.666
Tree sparrow	Intercept = 0	0.580	0.091	67	6.378	<0.001
	Slope = 1	0.458	0.109	67	-4.971	<0.001
Linnet	Intercept = 0	0.841	0.096	78	8.805	<0.001
	Slope = 1	0.313	0.143	78	-4.788	<0.001
Grey partridge	Intercept = 0	0.314	0.033	120	9.543	<0.001
	Slope = 1	-0.028	0.035	120	-29.011	<0.001

Table 4.3: The linear regression coefficients and significance tests of the intercept = 0 and the slope = 1 for the frequency of vigilance against feeding rate. There was no effect of food density on vigilance across the densities used in this analysis so the data was pooled.

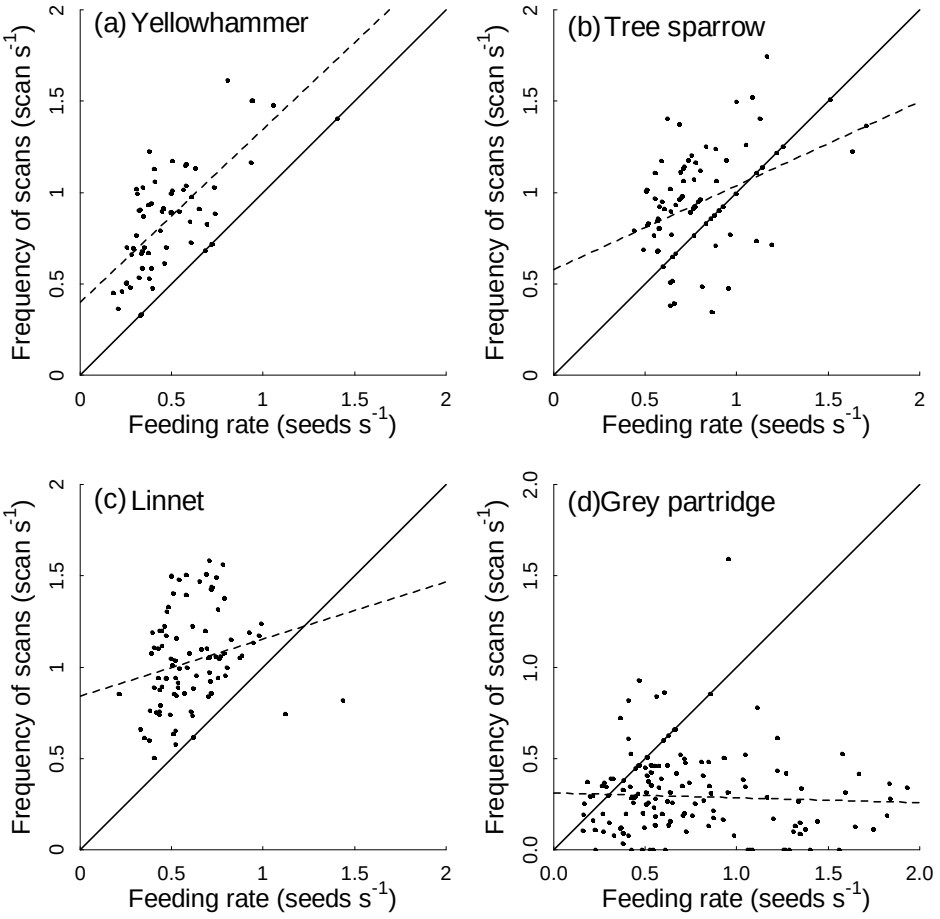

Figure 4.6: The frequency of vigilance scans (scans peck^{-1}) against the feeding rate (seeds s^{-1}) for: (a) yellowhammer (wheat); (b) tree sparrow (millet); (c) linnet (rape-seed); and grey partridge (wheat). The solid (━) line is the 1:1 line and the dashed (- - -) line is the linear trend for this data.

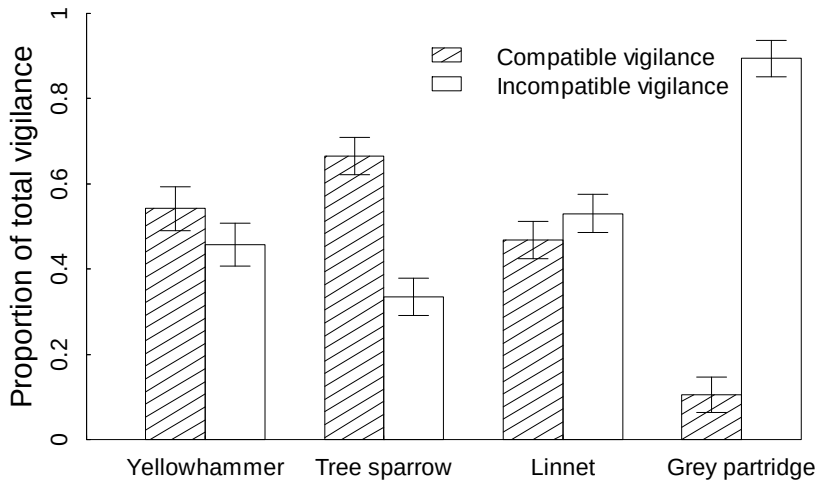

Figure 4.7: The time spent vigilant during the compatible portion of foraging (H_c) and incompatible portion of foraging (searching and H_x) for four species of granivorous birds. The error bars show the 95% confidence intervals.

The proportion of vigilance during compatible and non-compatible components of foraging (Fig. 4.7) were not significantly different for yellowhammer (paired t-test, t_{59}= 0.693, P = 0.491) and linnet (paired t-test, t_{92}= -1.884, P = 0.063), but was significantly greater in the compatible component (H_c) for tree sparrow (paired t-test, t_{82}= 6.978, $P < 0.001$) and the incompatible component (non-H_c) for grey partridge (paired t-test, t_{127}= -18.498, $P < 0.001$). Fig. 4.8 shows the proportion of H_c spent in a head-down posture, characterised as searching behaviour, for each of the four data sets and it can be seen that for three of the species (tree sparrow, linnet and grey partridge) greater than 50% of H_c is spent searching.

4.4.4 A functional response model with uniformly distributed vigilance

Based on the results of this analysis showing that handling time is consistently distributed between compatible handling time and non-compatible searching time I have derived two simple functional response models that includes vigilance, allows this vigilance to overlap with the H_c component of handling only and distributes vigilance uniformly between compatible handling and non-compatible searching (see appendix 2 for derivation).

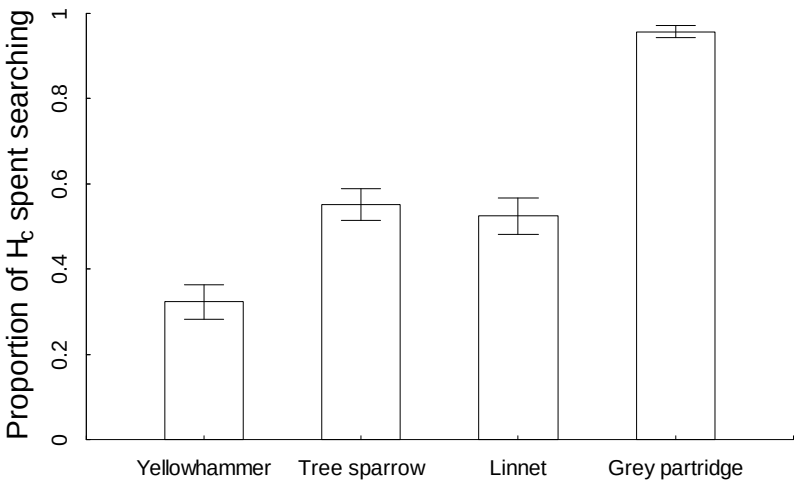

Figure 4.8: The proportion of time spent in a head-down posture during the H_c component of handling for four species of granivorous birds. The error bars show the 95% confidence intervals.

$$F = \frac{(1-v)aD}{1+aD(H_x(1-v)H_c)} \qquad \text{Model 1}$$

where F = feeding rate (prey s^{-1}), a = searching rate ($m^2 s^{-1}$), D = prey density (prey m^{-2}), H_x = incompatible handling time (s), H_c = compatible handling time (s) and v = proportion of time spent vigilant. By assuming that compatible and incompatible handling times are a fixed proportion of the total handling time a further simplified model can be derived

$$F = \frac{(1-v)aD}{1+(1-vp)aDH_t} \qquad \text{Model 2}$$

where H_t= total handling time (prey s^{-1}), and p = the proportion of handling time that is compatible with vigilance. Model 2 might be generally more applicable due to its simplicity, but model 1 will be important where the H_x and H_c components vary with prey density (Baker *et al*. 2010) and such variation can be incorporated directly into model 1.

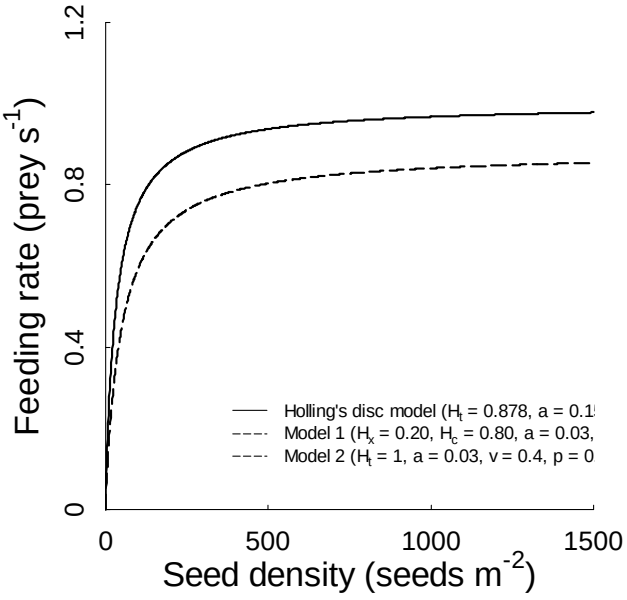

Figure 4.9: A comparison of the functional response predicted using models 1 & 2 (here producing an identical estimate), which distribute vigilance uniformly between compatible handling and searching, and the Holling's disc model. The models were parameterised for a hypothetical granivorous passerine to show how the models deviate in their predictions.

Figure 4.9 shows how the predictions of models 1 and 2 (which here produce identical predictions) differ from the Holling's disc model (Holling 1959) when parameterised using behavioural parameters representative of the passerines used in this study (i.e. ~ 40% of time spent vigilant, ~ 4:1 ratio of H_c:H_x (unpublished data – although varies with species and prey) and a searching rate of 0.03 $m^2 s^{-1}$ (i.e. Baker *et al.* 2009)). Allowing vigilance to be distributed uniformly between compatible handling time and incompatible searching time causes a lower estimate of feeding rate compared to the predictions of the Holling's disc model (parameterised similarly) and the vigilance model from Baker *et al.* (2010). This latter model predicts a similar fit to the disc model except at very low densities and is not shown in Fig. 4.9 as the differences are not discernable on the graph at this scale.

4.5 Discussion

The results of this study showed that the time spent vigilant per peck was consistently less than the compatible (H_c) component of handling for the tree sparrow and grey partridge, greater than H_c for linnet and yellowhammer. For linnet the time spent vigilant was on average greater than the H_c component of handling when H_c was low, suggesting compatible handling time was often of insufficient duration to accommodate the required vigilance. For the tree sparrow and grey partridge these results suggest that the negative consequences of routine vigilance could be avoided by accomplishing vigilance during the compatible component of foraging. However, for all species a high proportion of this vigilance occurs subsequent to food handling (Fig. 4.7) and, therefore, incurs a time-cost even though there is adequate time available to accommodate vigilance with little cost.

There was considerable time spent in a head-down posture (i.e. not fully vigilant) for all species observed here and it is this activity that appears to displace vigilance from the compatible portion of foraging to an incompatible portion (Fig. 4.8). Additionally, multiple scans per peck were observed for three species (Fig. 4.6) suggesting that head-up vigilance was conflicting with head-down behaviour, possibly searching. However, at asymptotic feeding rates searching time is expected to tend to zero as prey is superabundant so it appears surprising that handling is interrupted with any head-down behaviour. This head-down time could be interpreted as selective-searching behaviour, i.e. choosing the best morsel of food (Greig-Smith & Crocker 1984), and there is some evidence that increased choice can reduce the rate of decision making in foraging animals (Hutchinson 2005). For grey partridge the majority of vigilance appears to occur during non-compatible portions of the foraging bout, which might be due to short H_c times resulting from their ability to swallow seed whole, using their gizzard to crush the seed after ingestion (Hrabar & Perrin 2002): grey partridge spent ~95% of H_c in a head-down searching posture. A head-down posture may also allow for the monitoring of conspecifics for possible scrounging opportunities or to avoid aggressive interactions. However, such behaviours are more likely to be important when food resources are limited and their distribution is clumped, thus increasing the potential reward for time spent observing other foragers rather than searching.

The observed pattern and distribution of vigilance might be due to a trade-off

between vigilance and selective-searching that still maximises intake rate by reducing time wasted on unsatisfactory food items. It is unlikely that the short-term feeding rate of these species are constrained by digestive limits as each individual increases its predation risk by foraging in the open and should try to minimise its time spent in a high predation risk environment (Bednekoff & Lima 1994; Brown 1999). This can be achieved by maximising the feeding rate whilst on the foraging patch (Lima 1985) and retreating to cover when time-costs allow (Lima & Valone 1986; Valone & Lima 1987). Whilst it would still be optimal to be vigilant only during and search only once handling had ended, frequent short scans appear to increase the probability of detecting an approaching predator (Cresswell *et al.* 2003) and could help optimise foraging behaviour towards the rapidly changing demands of the local environment (i.e. competition from conspecifics) and, therefore, might provide a benefit over a single scan. Fritz *et al.* (2002) found that the instantaneous intake rate was reduced less when vigilance was divided into frequent short scans rather than a single scan of the same cumulative duration. The optimum routine for searching, compatible handling and vigilance could be explored further in simulation models and would be expected to vary considerably depending on the predation risk and food availability (i.e. Bednekoff & Houston 1994).

There was no relationship between any of the vigilance measures and seed density despite some previous expectation of a trend (Smart *et al.* 2008; Beauchamp *et al.* 2009; Baker *et al.* 2010). However, Beauchamp (2009) suggests that there is unlikely to be a significant correlation between vigilance and food density when the functional response is flat, as they were here. Group-size has been shown to have a negative correlation with vigilance, usually attributed to the 'many eyes' hypothesis (Pulliam 1973; Powell 1974) or the dilution effect hypothesis (Roberts 1996) and this has the potential to confound the results of vigilance studies where group size varies. However, we found no effect of group-size on any of the measures of vigilance, which might be because the group sizes were fairly constant throughout the experiments. There has been much discussion of the reverse effect, where food density would confound the results of experiments on the effect of group-size on vigilance, i.e. both feeding rates and group-size might increase with prey density and are expected to have opposing effects on vigilance, thus cancelling out any observed effect (Elgar 1989; Beauchamp 2009). However, the results here suggest that the potential for any confounding effect are minimal

where the foragers are feeding at their asymptotic rate. The lack of a relationship between seed density and feeding rate is likely to be because the seed densities were not low enough. As shown by the grey partridge data presented here the feeding rates only show a significant decline at quite low prey densities and this is largely a consequence of the easy foraging scenario presented in these experiments. In wild conditions food items are likely to be more difficult to find (i.e. partially buried) and the decrease in feeding rates would occur at higher densities; however, these conditions are difficult to replicate consistently in experimental conditions.

These results suggest that current functional response models that include vigilance are over simplifying the relationship between vigilance, handling and searching. It appears that searching is still an important component at high densities, at least in some circumstances (Fig. 4.8), and there has been no attempt to incorporate this additional searching parameter into these models. This appears to be important because additional searching displaces some of the vigilance from H_c into non-compatible components of foraging and thus incurs time-costs. To-date functional response models with vigilance assume that feeding rate will be maximised and do not consider the optimum pattern and distribution of vigilance. In most conditions animals are not foraging under time-constraints (Wolf, Hainsworth & Gill 1975; Bednekoff & Lima 1994; Ronconi & Burger 2008), even though they may want to reduce the time spent on open ground, and there will be a trade-off between feeding rate and vigilance (Brown 1999; Inger *et al.* 2006; Aubret, Bonnet & Bradshaw 2007). Future functional response models need to account for this additional head-down to time during H_c and assume that some vigilance will occur during non-compatible foraging. Here we derived two such models that assume a uniform distribution of vigilance between H_c and searching and showed the effect on the predicted feeding rate (Fig. 4.9). An approach such as this might predict observed functional responses more accurately than previous models that assume vigilance occurs preferentially during compatible handling time.

The effectiveness and utility of mechanistic functional response models lies in their simplicity and we must be careful not to incorporate more complexity than is necessary (Cox *et al.* 2006). Whether routine vigilance is a necessary component of the functional response models for these species is still open to debate because routine vigilance can always be reduced in response to time con-

straints (Brown 1999). To address these questions we require empirical studies of long-term feeding rates when foragers are experiencing time constrains to understand how these constraints affect vigilance and whether vigilance is necessary to predict feeding rates in the most critical circumstances, i.e. when starvation risk is high. However, vigilance can have an effect on foraging behaviour when prey is plentiful as predation risk, and consequently vigilance, can affect the spatial distribution of foragers as they try to optimise the trade-off between feeding rate and predation risk (Whittingham & Evans 2004; Duriez & Ferrand 2005; Cresswell 2008). Functional response models that include vigilance might provide a useful tool to explore such effects.

4.6 References

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Supplementary material

Additional supporting information may be found in the Appendix (Page 229 - 231)

Appendix 2. Derivation of functional response with mutually exclusive searching, uniformly distributed vigilance and partially overlapping handling and vigilance

Chapter 5

Towards a mechanistic model of prey handling: the attack component

5.1 Abstract

1. Handling time has been shown to vary with prey density yet this correlation is seldom included in mechanistic models of the functional response, where a suitable mechanistic model of handling is required. Handling time can be divided into an attack component and a processing component and each of these processes has a very different mechanistic relationship with prey density. The attack component will be effected by the changing distance between prey, with the attack time tending to decrease with increasing prey density as the prey become more closely packed.

2. Deriving a complete mechanistic model of handling time requires an understanding of the mechanistic processes underpinning each component. Here I focus on deriving a mechanistic model for the attack component of handling and testing its ability to predict the observed attack times of five granivorous bird species (yellowhammer, tree sparrow, linnet, chaffinch and grey partridge) when based on directly observed parameters.

3. I found that the relationship between attack time and prey density was negative for all species. I showed that a simple mechanistic model, incorporating the nearest-neighbour distance, speed of approach and the time to pick up a prey item, could predict the observed attack time as well as a regression model in most cases.

4. These results suggest that the attack component of handling time has a consistent but limited effect on total handling time for these species, with variations in the processing component explaining the greater proportion of the variation.

5. I have shown that prey density and distribution can affect the approach component of handling and derived a mechanistic model to predict this relationship. The model presented here provides a step towards a complete mechanistic model of prey handling and could be particularly effective for circumstances where the attack time is greater than processing time.

5.2 Introduction

Prey handling is an important component of foraging behaviour, often limiting the rate at which prey can be consumed and, therefore, affecting patterns of predation and resource depletion (Piersma *et al.* 1995). The functional response, i.e. the intake rate of a forager as a function of prey density (Holling 1966), is often defined in terms of the interactions between a searching component and a handling component (Holling 1959; Rogers 1972: also see Jeschke, Kopp & Tollrian 2002 for a review of type II functional response models and their parameters). In a type II functional response feeding rate increases at a decelerating rate as prey becomes more abundant, with the feeding rate approaching an asymptote at high prey densities. In many models the forager is considered handling-limited at these high prey densities and, therefore, the handling time sets the maximum feeding rate (Jeschke *et al.* 2002). Conversely, for some predators it is not handling that limits the feeding rate but the time taken to digest the prey once consumed (Holling 1966). The properties of these behavioural processes, their interactions with each other and their interactions with the foraging environment are crucial in determining the shape of the functional response. Mechanistic models, which describe a system as a function of the underlying processes (Cox *et al.* 2006), are commonly used to model functional response data, but are only valuable when these underlying processes and their interactions are realistically represented (Holling 1963).

In the context of mechanistic functional response models the relationship between handling time and prey density is important due to the assumptions made

by many such models. The Holling's disc model (Holling 1959) is often considered the null functional response model (Skalski & Gilliam 2001) and despite (or perhaps because of) its simplicity it is still the most commonly cited (Jeschke *et al.* 2002). This model considers the feeding rate as a function of the interaction between searching, handling and prey density, but has clear assumptions regarding the properties of these component processes (Holling 1959; Hassell, Lawton & Beddington 1976). One such assumption is that handling time is invariant with prey density yet there is ample evidence for consistent correlations between these parameters (Hassell *et al.* 1976; Giller 1980; Cooper & Anderson 2006; Smart, Stillman & Norris 2008; Okuyama 2010), including non-linear trends (Baker *et al.* 2010). The importance of this assumption is demonstrated in Smart *et al.* (2008) where the observed negative correlation between handling time and prey density was incorporated into the functional response model as a simple linear function of prey density, and caused a large decrease in the R^2 value and an overestimation of the asymptote compared with a model using a single mean value for handling. This suggests that the Hollings disc model was not an appropriate mechanistic description of the functional response of this species (corn bunting *Miliaria calandra* L).

Jeschke *et al.* (2002) commented that the Holling's disc model must be considered as phenomenological because not all of the parameters can be explained mechanistically. The handling parameter is a composite of many processes, including attacking, processing and digestion, and parameter estimates derived by fitting the disc model to observed data do not truly represent prey handling times. To incorporate the observed correlations between prey density and handling into the functional response models we need to understand this relationship mechanistically and to derive models that predict this relationship from quantifiable parameters. The correlation between handling time and prey density have been attributed to rate maximising and the marginal value theorem (Charnov 1976; Cook & Cockrell 1978; Giller 1980; Astrom, Lundberg & Danell 1990), where the time spent processing each prey item is dependent on the time taken to find the next item and the rate of gain from each prey (Stephens & Krebs 1986). Baker *et al.* (2010) divided the handling time into its constituent components (i.e. H_x (attack time) = the time from detection of the prey item to contact and H_c (processing time) = the time from contact to swallowing) and found a negative non-linear correlation for each component with seed density. Whilst the correlation of

H_c with prey density could be explained by marginal value theorem the H_x correlation is not affected by the same behavioural processes and requires a different explanation. Baker *et al.* (2010) suggested that this correlation is a consequence of the increasing distance among prey items as prey density decreases causing the H_x component to become progressively longer as prey are attack over greater distances. This phenomenon might provide a mechanistic function that links the H_x to prey density and provides a mechanistic model for the H_x component of prey handling.

Here I focus on deriving a mechanistic model for the attack component of handling and testing its ability to predict the observed attack times of five granivorous bird species. I have derived a simple mechanistic function that describes the relationship between prey density and H_x based on the assumption that the H_x component of handling is related to the density and spacing of prey items; the H_x function can then be used to estimate H_t. I test the assumptions of this model using functional response data gathered from five species of granivorous farmland birds, grey partridge *Perdix perdix* L, chaffinch *Fringilla coelebs* L, linnet *Carduelis cannabina* L, tree sparrow *Passer montanus* L and yellowhammer *Emberiza citrinella* L. Here I: (i) test the relationship between handling time (H_t) and prey density, including the sub-processes of H_x and H_c; (ii) test the ability of a mechanistic model of H_x (based on directly observed parameters) to predict the observed H_x and H_t (i.e. $H_t = H_x + H_c$); and (iii) test which component process (H_x or H_c) explains the greatest proportion of the variation in the total handling time (H_t). I discuss the importance of handling time for predicting the functional response and the need for complete mechanistic models of handling time in functional response models.

5.3 Methods

Granivorous birds are good model foragers for studying the component processes of foraging behaviour for several reasons. Firstly they exhibit fairly distinct behaviours for each component of foraging (Smart *et al.* 2008; Baker, Stillman & Bullock 2009; Baker *et al.* 2010) enabling accurate estimation of each component process. Secondly, the choice of granivorous foragers removes some of the difficulties encountered with other predator-prey systems, i.e. mobile prey (Cooper & Anderson 2006; Coleman 2008) or grazers / browsers taking multiple

bites whilst still handling (Spalinger & Hobbs 1992; Hobbs *et al.* 2003; Fortin *et al.* 2004). Thirdly, many of these bird species retreat to cover when not foraging (Whittingham & Evans 2004) and, therefore, are not considered to be digestion-limited over the duration of a foraging bout (i.e. < 10 prey items). And finally, prey capture is seldom unsuccessful when the seeds are easily accessible to the bird (DJB per. obs.).

5.3.1 Defining handling time

Definitions of handling times vary, sometimes including digestive processes (Hollings 1959) and sometimes including only the time spent capturing and ingesting the prey (Stillman & Simmons 2006; Baker *et al.* 2010). Holling (1966) defined handling time as a function of the time spent: (i) pursuing and subduing each prey item; (ii) eating each prey item; and (iii) in 'digestive pause'. Defined as such, the handling component of the Holling's disc model becomes a composite of prey handling and prey digestion and, therefore, handling can no longer be described mechanistically. Jeschke *et al.* (2002) highlight the fact that prey handling is an active process whilst digestion is a background process, and that a predator can still search and handle prey whilst digesting. The digestion process affects the desire or necessity to find more food, but does not in itself necessarily exclude these activities. At this point it is important to distinguish between long-term and short-term intake rate as a forager might be digestion-limited over the long-term but handling-limited over the short term. This situation might occur when prey items are small and quick to consume and, therefore, many prey items must be consumed before a state of satiation is reached. Because I will be measuring the foraging behaviour over a short time interval and, therefore, the birds are not likely to be satiated during that time only the first two components of Holling's definition are appropriate. Given that the 'prey' items in this study are seeds I define handling time as, the time taken to: (i) attack each prey item (H_x); and (ii) process and consume each prey item (H_c).

5.3.2 A mechanistic model of attack time

Under the definition of handling used here, and similarly with Holling's (1959) definition, the H_x component of handling is dependent on the distance over which a prey item is detected, and this is a function of prey density, the speed of ap-

proach and the time to pick up the item. There will be a maximum detection distance set by sensory limits, but for granivorous foragers I assume this occurs only at very low prey densities not often encountered in the wild. The following model assumes that the forager always chooses the closest prey item, which they detect with certainty, that the prey is immobile and clearly visible, and that the prey is randomly distributed. The expected nearest-neighbour distance (D_E) between randomly distributed objects is given by the function (Clark & Evans 1954; Hobbs *et al.* 2003)

$$D_E = \frac{0.5}{\sqrt{\frac{n}{A}}} \tag{1}$$

where A = area and n = number of objects. Because the forager is present in the patch and I am interested in knowing the expected nearest-neighbour distance from the forager's perspective it is necessary to include the forager as one of the objects ($+\frac{1}{A}$)

$$D_E = \frac{0.5}{\sqrt{\frac{n}{A}+\frac{1}{A}}} \tag{2}$$

The density of objects present in a patch (excluding the forager) of area A is given by

$$D = \frac{n}{A} \tag{3}$$

where D = prey density (prey m^{-2}), and this can be substituted into equation 2. The H_x component of handling time is a function of the distance over which prey items are detected and the speed with which the forager approaches the prey once detected. However, there is a minimum H_x time because there must always be some time spent making contact with the prey item even if prey is superabundant (e.g. bending down to pick up the item). This minimum value can be estimated from the minimum observed values of H_x when prey was superabundant. If we assume that the forager always targets the closest prey item then the H_x component of handling is given by

$$H_x = \left(\frac{0.5}{S\sqrt{D+\frac{1}{A}}} \right) + H_{x\_min} \tag{4}$$

where S = travel speed ($m\ s^{-1}$) and H_{x_min} = the minimum value of H_x. Equation 4 is referred to as model model 1 in the text. The total handling time (H_t) is given by the sum of the component processes (H_x and H_c)

$$H_t = H_x + H_c \tag{5}$$

Substituting equation 4 into equation 5 gives the total handling time which is a function of prey density due to our derivation of H_x

$$H_t = \left(\frac{0.5}{S\sqrt{D+\frac{1}{A}}} \right) + H_{x\_min} + H_c \tag{6}$$

Equation 6 is referred to as model 2 in the text and is not a fully mechanistic model because I make no attempt here to explain mechanistically the correlation between seed density and H_c. However, a mechanistic model of H_c could be substituted for into equation 6 giving a complete mechanistic model of prey handling.

5.3.3 Functional response and handling time experiments

Three functional responses and the associated handling time measurements were obtained for three species of granivorous farmland birds (yellowhammer *Emberiza citrinella* L, tree sparrow *Passer montanus* L and linnet *Carduelis cannabina* L) feeding on wheat (yellowhammer), millet (tree sparrow) and rapeseed (linnet). Additionally, two previously published functional responses of chaffinch feeding on rapeseed (Baker *et al.* 2009) and grey partridge feeding on wheat were analysed to provide additional data (Baker *et al.* 2010).

The unpublished functional response experiments were conducted as follows: the linnet experiment was conducted at Woodborough Hill Farm in Wiltshire between the 1^{st} and 3^{rd} February 2006: the tree sparrow experiment was conducted at Easton Farm between the 5^{th} and 7^{th} April 2006; and the yellowhammer experiment was conducted at Stanton St Bernard Farm between the 22^{nd} March 2006 and the 6^{th} April 2006. The protocol of these experiments closely follows that of Smart *et al.* (2008) and Baker *et al.* (2009) but will be briefly summarised here. The experiments were conducted on plywood and concrete platform measuring 1m x 1.5m and dyed and textured to mimic the surrounding soil. The birds

were presented with different densities of scattered seeds (125, 250, 500, 1000, 2000, 3000, 4000 seeds m^{-2}) in a random sequence and three replicates were carried out for each density. The experiments were conducted between 09:00 and 15:00 h and each replicate was filmed using a Canon 3CCD XL1 video camera (www.canon.co.uk) for at least 15 minutes from a distance of approximately 30m; filming was along the length of the platform. Outside of the periods of the experiment the platforms were covered and seed scattered on top to keep the birds attracted to the area.

5.3.4 Analysis of functional response behavioural experiments

The video footage was downloaded onto a PC and analysed using a purpose-built event recorder. During the analysis I was careful to analyse sequences where large groups of birds were foraging on the feeding platforms simultaneously to avoid including the same individual more than once. These sequences were quite easy to find here as the seed densities used were relatively high and the birds quickly flocked to the platform. Any seed density for which there was ≤ 10 individual birds recorded foraging was excluded from the analysis and, therefore, some densities are excluded. The feeding rate was measured from the frame before the bird made contact with the first seed until the frame before the bird made contact with the last seed for a minimum of five pecks. Here I choose to define handling time as the time taken to capture and ingest the seed, and explicitly exclude digestive processes that might occur after ingestion. Handling time was divided into two components, an approach component (H_x) and a processing component (H_c). H_x was measured from the video frame at which the bird began moving towards the target seed, shown by a distinct change in behaviour, to the frame before contact with the target. The processing component (H_c) was measured from the frame before contact with the target seed until the seed was consumed, which was determined through the movement of the bill. Travel speed (S) was calculated as (H_x distance)/(H_x time) and the distance over which the seed was targeted was measure using the method of Baker *et al.* (2010). Here a screen capture of the start and finish position of the bird was imported into Photoshop CS4 (www.adobe.com). A grid layer was placed over the top of the video images and the grid was warped using the perspective tools to fit over the shape of the platform; the bird's coordinates could then be read from the grid. The group size was recorded at each peck for all individuals and the mean group size over a

foraging bout used in the analysis to test for a group size effect. The functional response data from Baker *et al.* (2009) and Baker *et al.* (2010) were reanalysed to obtain these extra handling time parameters.

5.3.5 Statistical analysis

The relationship between feeding rate and prey density was explored using linear-mixed effects models, with trial as random factor, and the most likely model was judged using bias-adjusted Akaike Information Criterion (AIC_c). The residuals were checked for normality and linearity and these assumptions were met for all functional response data. Group size was included as an explanatory variable in the initial model and removed where not significant. The relationship between handling time, including its component processes, and seed density were explored using linear mixed models, with trial as random factor. For several of these relationships the most likely model included a natural log transformation of seed density resulting in a non-linear relationship, as hypothesised in this study. The residuals were checked for normality and linearity and for some of the data a natural log transformation of the response variable was required. Group size was included as an explanatory variable in the initial model for all components and removed where non-significant. The influence of H_c and H_x on the total handling time (H_t) was explored using general linear models, as above, and the component that explained the greatest degree of variation was judge using the adjusted-R^2 value.

5.4 Results

5.4.1 The functional response

I found no significant effect of prey density on the feeding rates of yellowhammers foraging for wheat (Fig. 5.1a) (b = 0.000006, t_{63} = 0.328, P = 0.744), tree sparrows foraging for rapeseed (Fig 5.1b) (b = - 0.000008, t_{81} = -0.399, P = 0.691) and linnets foraging for millet (Fig 5.1c) (b = - 0.000014, t_{96} = -1.034, P = 0.304) at the densities used in this study. Figs 5.1d and 5.1e show the functional response for chaffinches (Baker *et al.* 2009) foraging for rapeseed and grey partridge (Baker *et al.* in press) foraging for wheat seeds. There was no effect of seed density on the feeding rate of chaffinches across these densities, but grey

partridge feeding rate was significantly positively correlated with seed density, as reported by the authors.

Group size was included as an explanatory variable in the initial model for each of the species but was not significant in any case. I tested for a correlation between group size and seed density for all species (except grey partridge where the group size was held constant). The correlation was non-significant in all cases except tree sparrow where a significant positive correlation exists (b = 0.00013, t_{81} = 0.523, $P < 0.0001$).

5.4.2 The relationship between handling times and prey density

Table 5.1 summarises the observed trends for H_t, H_x and H_c with seed density for granivorous farmland birds. The data presented in Baker *et al.* (2009) were reanalysed to obtain estimates of the H_x and H_c components of handling time that were not included in the original analysis. The results are given for the grey partridge data using only the bare soil treatment for consistency with the other data and, therefore, the results differ slightly from those reported in Baker *et al.* (2010) where the treatments were combined when there was no effect of treatment (bare soil & stubble).

H_t was positively correlated with log (density) for linnet (Fig. 5.2c) (b = 0.159, t_{97} = 5.246, $P < 0.0001$). Log(H_t) was positively correlated with log (density) for tree sparrow (Fig. 5.2b) (b = 0.128, t_{81} = 5.286, $P < 0.0001$) and chaffinch (Fig. 5.2d) (b = 0.091, t_{102} = 2.833, P = 0.006), and negatively correlated for grey partridge (b = -0.145, t_{140} = -6.919, $P < 0.0001$). H_t was not correlated with seed density for yellowhammer (Fig. 5.2a) (b = 0.00001, t_{63} = -0.312, P = 0.756). H_x was negatively correlated with log (density) for yellowhammer (Fig. 5.3a) (b = -0.016, t63 = -3.464, P = 0.001), chaffinch (Fig. 5.3d) (b = -0.0113, t_{102} = -3.741, P = 0.0003) and grey partridge (Fig. 5.3e)(b = -0.061, t_{140} = -9.569, $P < 0.0001$) and with seed density for tree sparrow (Fig. 5.3b) (b = -0.00004, t_{81} = - 2.262, P = 0.026) and linnet (Fig. 5.3c) (b = -0.00001, t_{97} = - 3.251, P = 0.002). H_c was positively correlated with seed density for linnet (Fig. 5.4c) (b = 0.00012, t_{97} = 5.873, $P < 0.0001$) and with log(density) for chaffinch (Fig. 5.4d) (b = 0.193, t_{102} = 3.247, P = 0.0016). Log(H_c) was positively correlated with log(density) for tree sparrow (Fig. 5.4b) (b = 0.00013, t_{81} = 5.267, $P < 0.0001$). A negative correlation

				Relationship between handling time and seed density		
Forager species	Habitat	Density Range	Prey	H_t	H_x	H_c
Emberiza citrinella	Bare soil	250 - 4000	Wheat seed	None	Negative	None
Passer montanus	Bare soil	125 - 4000	Millet seed	Positive	Negative	Positive
Carduelus cannabinna	Bare soil	125 - 4000	Rapeseed	Positive	Negative	Positive
Fringella coelebs	Bare soil	25 - 1600	Rapeseed	Positive	Negative	Positive
Perdix perdix	Bare soil	5 - 400	Wheat seed	Negative	Negative	Negative
Perdix perdix	Stubble	5 - 400	Wheat seed	Negative	Negative	Negative
Miliaria calandra	Bare soil	125 - 400	Wheat seed	Negative	NA*	NA*

* Not measured in Smart *et al.* (2008)

Table 5.1: The relationships between handling time, including the component processes, handling time and prey density for six species of granivorous birds. H_t = total handling time (H_x + H_c), H_x = approach time (detection to contact), H_c = processing time (contact to ingestion) and density range = seed m^{-2}.

between H_c and log(density) was found for grey partridge (Fig. 5.4e)(b = -0.057, t_{140} = -3.544, P = 0.0005), but there was no correlation for yellowhammer (Fig. 5.4a) (b = -0.000007, t_{63} = -0.019, P = 0.985).

The group size was included in the initial model for each measure of handling time, but was only significant for the H_x component for linnet (b = 0.0015, t_{96} = 2.069, P = 0.0412).

5.4.3 Predicting H_x with a mechanistic model (model 1)

I tested the ability of model 1 to predict H_x using experimentally measured values for H_{x_min} and S and compared this model with the linear regression models (H_x = seed density) presented above. The linear regression model will always go through the observed data, but model 1 parameterised using experimentally measured parameter estimates might not provide a good fit if the model is mechanistically flawed. Table 5.2 shows the R^2 and AIC values for these comparisons. For the H_x component of handling model 1 explained more variation than the linear regression model for yellowhammer, but less variation for the other data. The Akaike weights were used to compare the likelihood of each model relative to the other and consistently showed that there was little difference separating the two models. Model 2 was used to predict the total handling time (H_t) using the mechanistic H_x function (model 1) and with the assumption that H_c is invariant with prey density. This model used experimentally measured parameter values for H_c, H_{x_min} and S. The linear regression model provided a better fit to the observed data than model 2 for all species showing that the H_x component is not contributing much to the overall variation in H_t.

5.5 Discussion

In this study on mechanistic models of prey handling I found that the attack component (H_x) of handling time was consistently negatively correlated with prey density (Table 5.1) and that a mechanistic model of the attack component produced a similar fit (judge using Akaike weights) to the observed data for several species. This suggests that this model is a good mechanistic description of the attack process and is the first step in developing a complete mechanistic model of prey handling. Due to the variation in observed handling times neither a linear

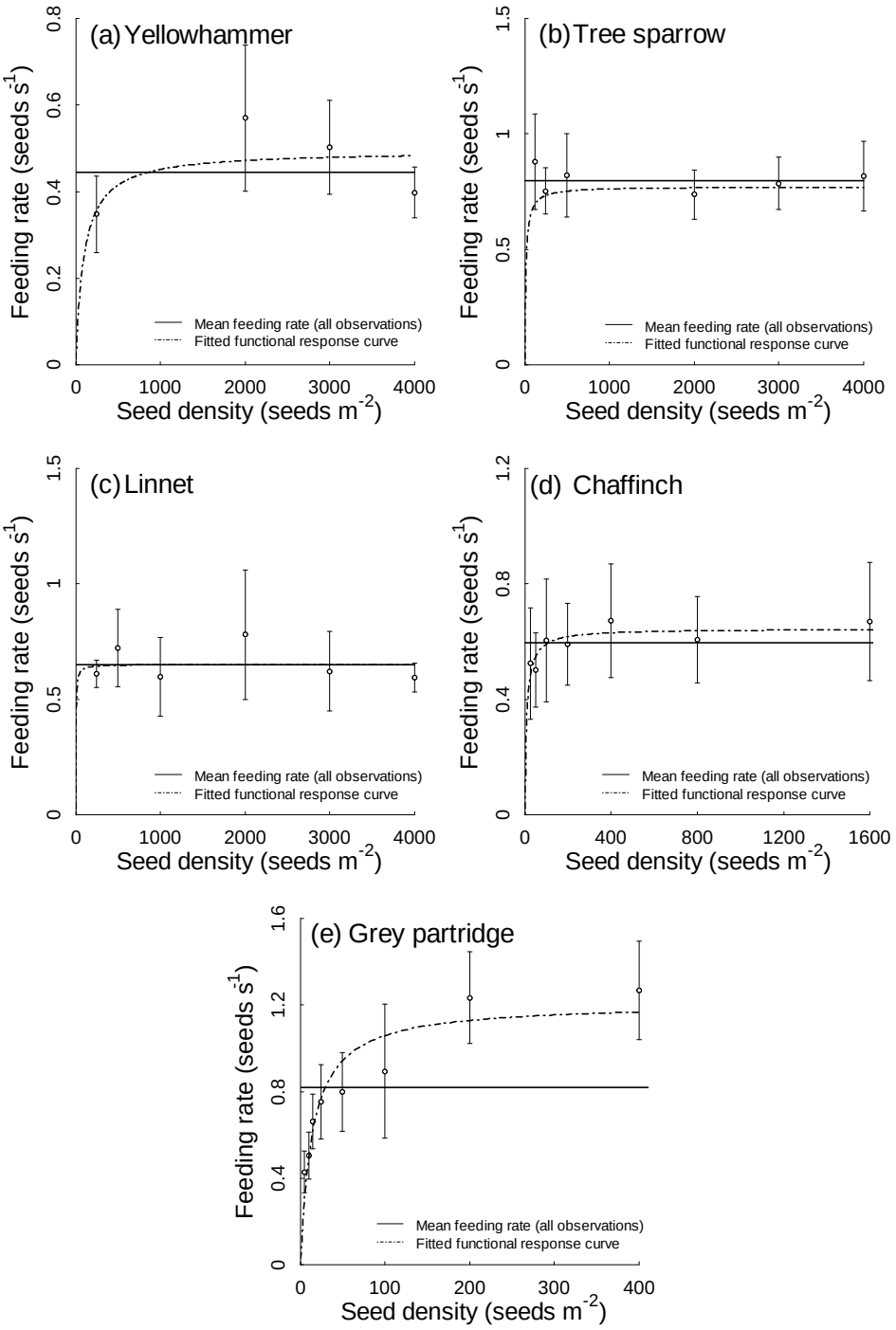

Figure 5.1: The effect of prey density on the feeding rate (functional response) of: (a) yellowhammers; (b) tree sparrows; (c) linnets; (d) chaffinches; and (e) grey partridges. Each graph shows the observed feeding rate (± 95% C.I.) with the fitted functional response curve (- - -) (non-linear least square regression of the function $F = \frac{aD}{b+D}$, where a = half-asymptote, b = asymptote and D = density) and showing the mean feeding rate for all densities (—).

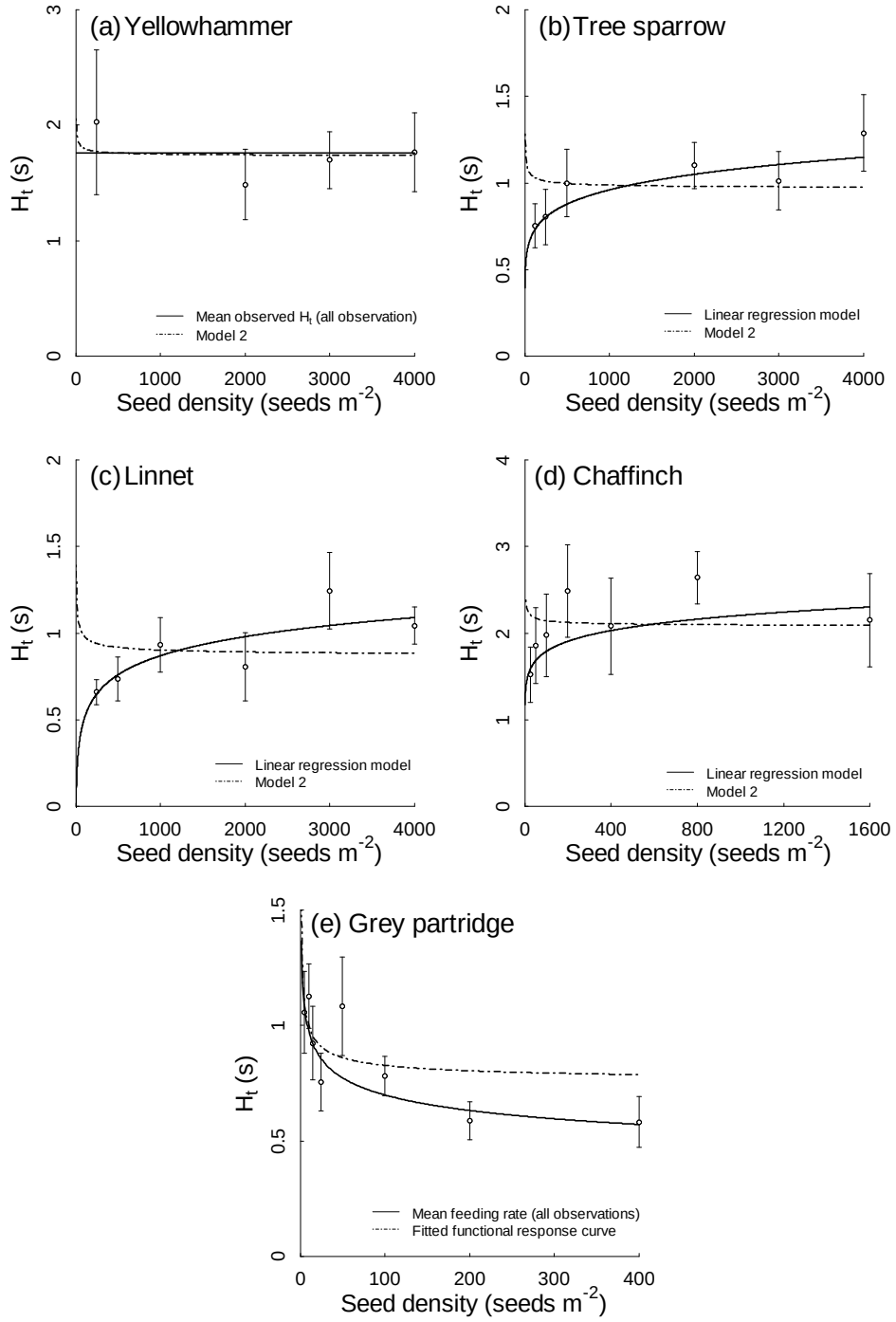

Figure 5.2: The effect of prey density on the total handling time (H_t) of: (a) yellowhammers; (b) tree sparrows; (c) linnets; (d) chaffinches; and (e) grey partridges. Each graph shows the observed H_t (± 95% C.I.) and the correlation with prey density (—) where a significant relationship exists; if no significant relationship exists then the mean for all data is shown. The total handling time predicted using model 2 is also shown (- - -), with the parameters of S (approach speed), H_{x_min} (approach distance) and H_c (processing time) measured experimentally.

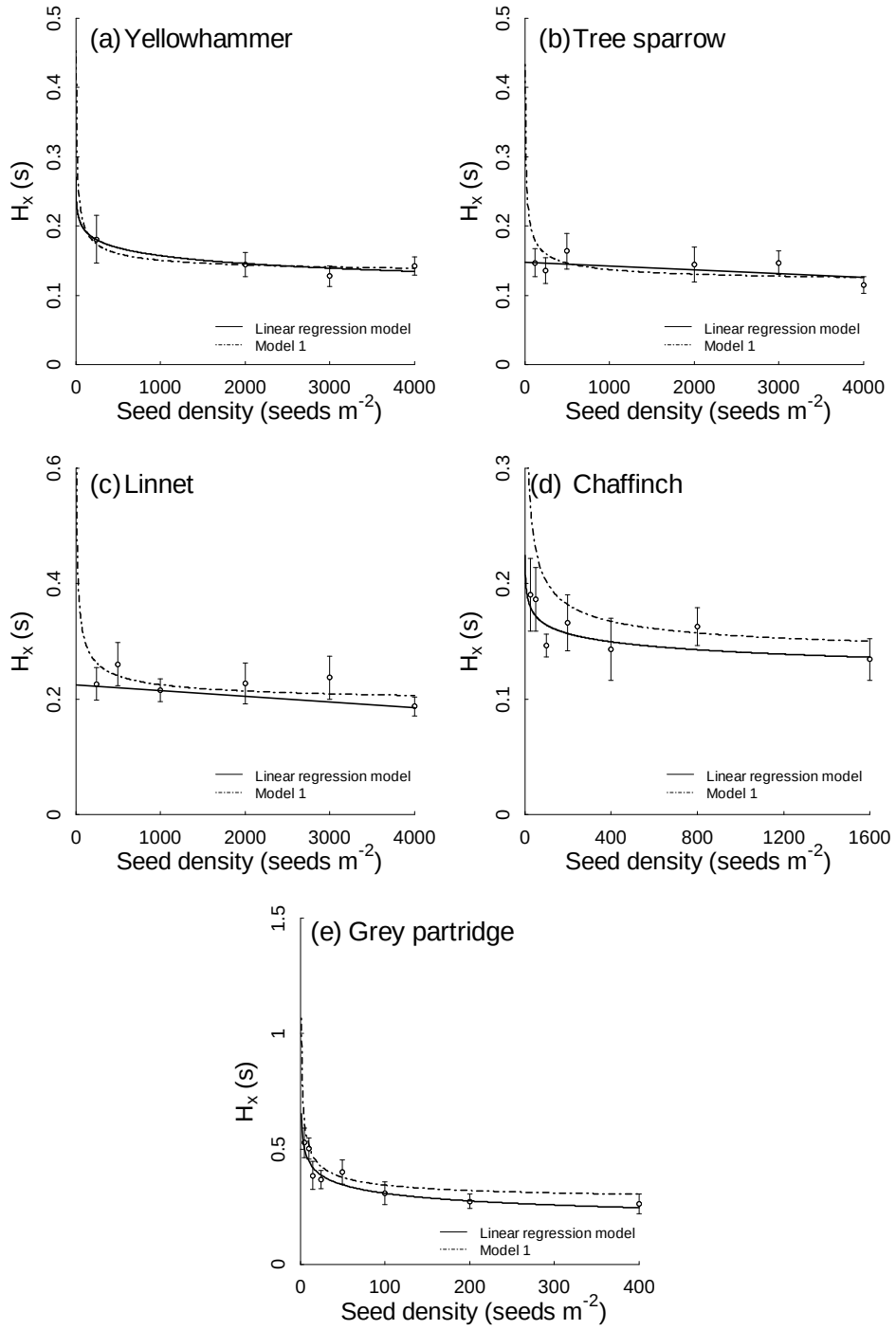

Figure 5.3: The effect of prey density on the approach component of handling time (H_x) of: (a) yellowhammers; (b) tree sparrows; (c) linnets; (d) chaffinches; and (e) grey partridges. Each graph shows the observed H_x (± 95% C.I.) and the correlation with prey density (—) where a significant relationship exists; if no significant relationship exists then the mean for all data is shown. The approach component of handling time (H_x) predicted using model 1 is also shown (- - -), with the parameters of S (approach speed) and H_{x_min} (approach distance) measured experimentally.

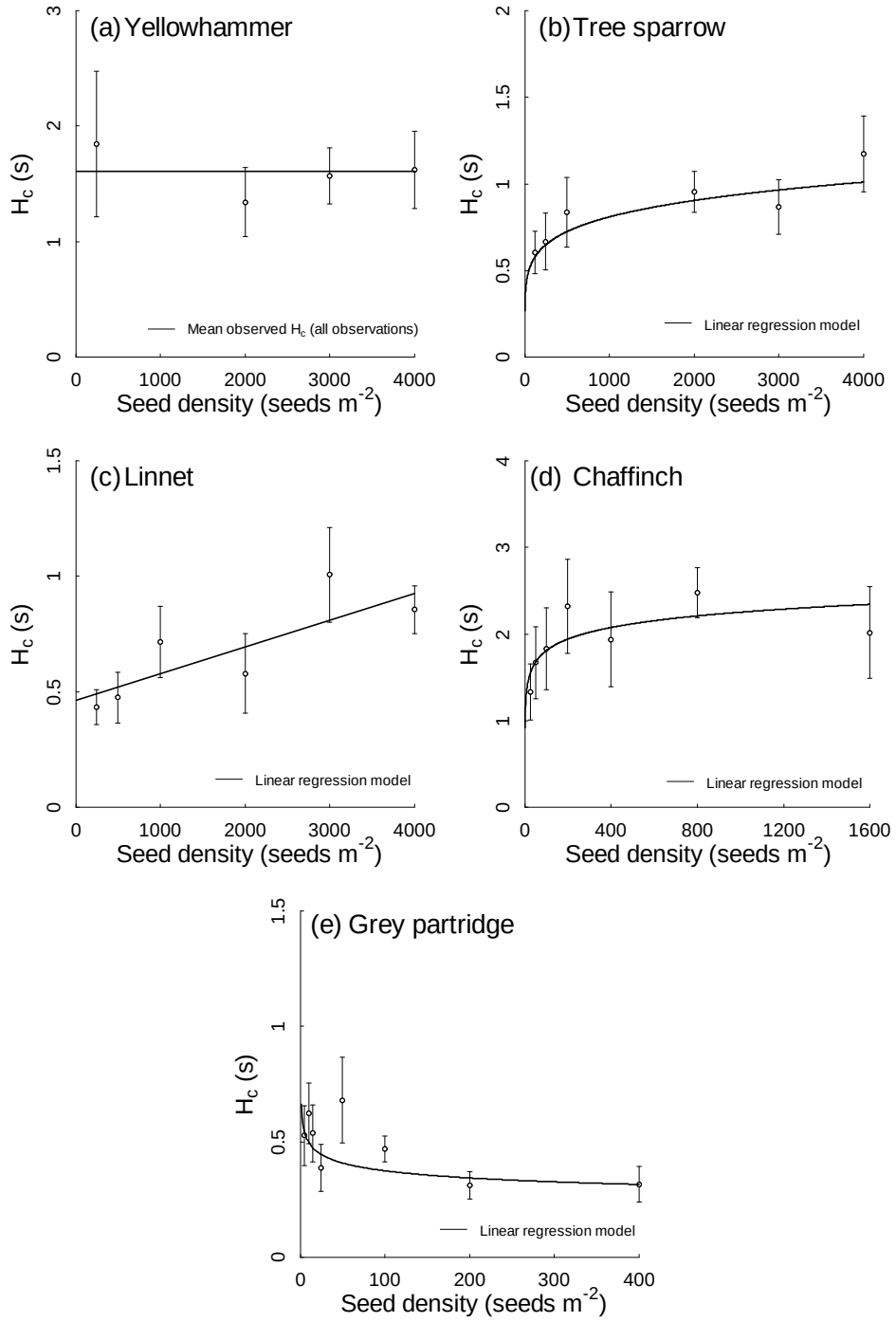

Figure 5.4: The effect of prey density on the processing component of handling time (H_c) of: (a) yellowhammers; (b) tree sparrows; (c) linnets; (d) chaffinches; and (e) grey partridges. Each graph shows the observed H_c (± 95% C.I.) and the correlation with prey density (—) where a significant relationship exists; if no significant relationship exists then the mean for all data is shown.

Functional response		Model	Coefficients		Model parameters			R^2	K	RSS	AIC_c	$\triangle_i$	w_i
			b_0	b_1	S	H_{x_min}	H_c						
Yellowhammer	H_t^*	Reg. model*	1.760	0				0.000	3	44.896	2.492	0	0.541
		Model 2			0.688	0.128	1.6	0.006	4	44.628	2.822	0.329	0.459
	H_x	Reg. model	0.271	-0.016				0.160	3	0.118	0.497	0.00003	0.500
		Model 1			0.688	0.128		0.156	3	0.119	0.497	0	0.500
Tree sparrow	$\log(H_t)$	Reg. model*	-0.924	0.128				0.210	3	7.037	0.622	0	0.540
		Model 2			0.702	0.115	0.851	-0.058	4	9.423	0.944	0.322	0.460
	H_x	Reg. model	-0.907	-0.00004				0.037	3	0.115	0.384	0	0.500
		Model 1			0.702	0.115		-0.153	3	0.138	0.385	0.001	0.500
Linnet	H_t	Reg. model*	-0.225	0.159				0.221	3	8.774	0.567	0	0.536
		Model 2			0.424	0.188	0.678	-0.059	4	11.925	0.855	0.289	0.464
	H_x	Reg. model	0.245	-0.00001				0.783	3	0.304	0.603	0	0.502
		Model 1			0.424	0.188		0.017	3	0.325	0.622	0.019	0.498
Chaffinch	$\log(H_t)$	Reg. model*	0.165	0.091				0.033	3	77.168	2.397	0	0.546
		Model 2			0.724	0.133	1.941	-0.043	4	83.204	2.769	0.372	0.454
	H_x	Reg. model	0.222	-0.011				0.185	3	0.185	0.305	0	0.501
		Model 1			0.724	0.133		-0.675	3	0.352	0.310	0.005	0.499
Grey partridge	H_t	Reg. model*	0.310	-0.145				0.177	3	15.059	0.514	0	0.519
		Model 2			0.624	0.133	0.483	0.142	4	15.700	0.662	0.148	0.482
	H_x	Reg. model	0.604	-0.061				0.395	3	1.519	0.247	0	0.501
		Model 1			0.624	0.133		0.285	3	1.797	0.253	0.006	0.499

Table 5.2: The comparison of a linear regression model and the mechanistic models (model 1 & model 2) ability to describe the observed relationship between total handling time (H_t) and prey density and approach time (H_x) and prey density. The parameters of S (approach speed), H_{x_min} (approach distance) and H_c (processing time) measured experimentally. K = parameter number, RSS = residual sum of squares, AIC_c = bias-adjusted Akaike Information Criterion, Δ_i = difference between AIC_i and lowest AIC and w_i = Akaike weights. The Akaike weights (w_i) are used to compare the likelihood of each model relative to the other (Edwards *et al.* 2007).

regression model nor the mechanistic model explained much of the variation in H_x. However, model 1 captured the shape of the observed relationship between prey density and H_x using experimentally measured behaviour parameters alone and, therefore, could be used to predict this relationship from measurements of only two behavioural parameters (H_{x_min} (i.e. at high prey densities) and S).

The processing component (H_c) was correlated to a greater degree with total handling times (H_t) for these species and explained more variation. This suggests that H_x is contributing only slightly to the observed variation in the total handling time and consequently model 2 produced a poor fit to the observed H_t data because the H_c component was held constant throughout. A major *a priori* assumption of model 2 is that H_c is invariant with prey density, as assumed by most functional response models, and that H_x contributes most of the variation in H_t. However, for the most foragers this is unrealistic and therefore a mechanistic model of the H_c component is required, which will give us a complete mechanistic model of handling.

The H_c component was found to be significantly positively correlated with log (seed density) for tree sparrow and chaffinch, and with untransformed seed density for linnet. Most studies confound the effects of H_x and H_c, even when acknowledging the potential affect these processes could have individually on the overall handling time (Cooper & Anderson 2006). However, most handling time studies appear to support the general trend that the H_c component is longer than the H_x component (Giller 1980; Ulenaers, van Vessem & Dhondt 1992; Cooper & Anderson 2006; Nilsen *et al.* 2009) even when this is not explicitly studied. Because the processing time dominates handling for most foragers it is likely that the overall trends reported for handling are representative of the underlying processing trend and, therefore, most H_c trends appear to be negatively correlated with prey density (Giller 1980; Cooper & Anderson 2006; Okuyama 2010). The marginal value theorem would predict that less time is spent handling as prey availability increases, assuming diminishing returns with time handling a single prey item (Stephens & Krebs 1986), thus contradicting the positive correlations observed here for three data sets.

However, when foraging in groups on an unpredictable prey supply there might be an incentive to consume prey items faster when the density is lower to avoid losing opportunities to other foragers (Stillman *et al.* 2000). Such a mechanism might be expected when the forager is trying to maximise its intake

rate over the duration of a foraging bout and might be increasingly likely as prey availability decreases. Courant & Giraldeau (2008) showed that when feeding on cryptic prey the presence of a conspecific reduced the searching rates for nutmeg mannikins *Lonchura punctulata* and significantly increased the number of detection errors, thus, longer searching times would reduce the feeding rate under such conditions and a reduction in handling time would be necessary to compensate. Although these species can handle and search simultaneously handling is most often accomplished whilst stationary (DJB per. obs.), perhaps because simultaneous handling reduces the detection rates or because vigilance can be accommodated cost-free during handling (Cowlishaw *et al.* 2004). This effect will be more likely to occur when time-constraints or foraging are present, such as increased competition for limited resources at low prey densities due to the presence of conspecifics (Dolman 1995; Courant & Giraldeau 2007). Group-size was only significant for one behaviour component of one species here and this might have been because the group-sizes were fairly constant throughout the experiments, yet as prey density decreases the number of prey per forager decreases and this could induce greater scramble competition over increasingly limited resources. This effect could be studied using lone foragers or by maintaining a constant forager to prey ratio, although this may induce confounding factors such as group-size vigilance effects.

Another possible explanation is that handling time is correlated with anti-predator vigilance, and as prey density decreases an increasing amount of time must be devoted to searching to maximise feeding rate, thus reducing vigilance levels, with the resultant decrease in handling time (Beauchamp 2009). Johnson, Giraldeau and Grant (2001) found a positive correlation between total handling time and prey density of house sparrows *Passer domesticus* and concluded that animals adjust handling to avoid interference from conspecifics, which was greater at higher prey densities. However, the reverse could also be true, with increased monitoring of conspecifics at higher densities reducing feeding rates and allowing for longer handling times. Of the remaining two H_c trends one showed no correlation with seed density (yellowhammer) and one shows a negative correlation with log(seed density) (grey partridge). The former had several seed densities missing because too few yellowhammers fed at these densities and this might mask a pattern. The latter shows a non-linear trend affecting the very low densities, which could be explained as a consequence of maximising the gain

from each seed, i.e. as predicted by the marginal value theorem.

It is clear that these correlations between handling time, including its sub-components, and prey density are important in shaping the functional response. Whilst the H_x component has been shown here to be largely a function of the nearest-neighbour distance when the prey are randomly distributed, the H_c component is likely to be more complex and requires much experimental research to disentangle the effects of prey density, competition, prey type and numerous other behavioural and environmental parameters on the time spent processes each prey (i.e. Paszkowski & Moermond 1984; Norris & Johnstone 1998; Cooper & Anderson 2006). The overall trends for the H_c component appear highly variable at present (Table 5.1) and, therefore, it is not possible to derive a mechanistic model to predict such trends when the underlying mechanism responsible for such patterns are not understood. The marginal value theorem might help explain some of the variation, however, many of the seed types used here have very short handling times and a steep gain function, which means that any variation in processing times will be slight. For example, many seeds are swallowed whole, or only partially crushed before swallowing, once the husk has been removed (Hrabar & Perrin 2002; Van Der Meij & Bout 2004), with the bird relying on the gizzard to break up the seed during digestion (Hrabar & Perrin 2002). In such circumstances there is a single-step gain function, where no energy is gained during dehusking but the maximum gain is achieved by immediately swallowing the seed (Stephens & Krebs 1986). This might limit the applicability of the marginal value theorem to such species and an alternative mechanism for the correlation between H_c and prey density must be proposed. For birds with smaller gizzards breaking the seed into smaller pieces probably aids digestion and helps to reduce digestive bottlenecks (Van Gils *et al.* 2003), which are more probable when prey density is high, and here there might be a benefit from more careful processing.

Mechanistic functional response have great potential for applied research into the effects of environmental changes on bird populations when prey is the limiting factor (Stephens *et al.* 2003; Norris 2004; Sutherland 2006) as they can directly link resource availability to population persistence. However, these models must capture the underlying behaviour in a suitably realistic manner in order for the model to predict with confidence the effects of environmental changes on populations. Here I have broken handling time into separate components and derived a simple mechanistic model that can predict the observed value of the at-

tack component. I have examined the observed correlations between prey density and processing time and suggested several possible mechanisms for the observed trends; however, much more research will be required before a mechanistic model of this component can be derived. It is important that the assumptions of mechanistic models are tested in such a manner, as originally laid out by Holling (1963), and that models are derived that avoid obviously incorrect assumptions and strive for mechanistic descriptions of each parameter. There is still much research required to understand the functional responses of even a simple predator-prey system such as granivorous birds. The Holling's disc model has been used in spatial depletion models to link resource abundance to patch use, prey depletion and over-winter survival (i.e. Robinson 1997; Gill, Sutherland & Norris 2001; Butler *et al.* 2010) yet this model has clearly erroneous assumptions and the consequences of these assumptions are often unknown. Whether handling time is a key rate limiting parameter, or digestive constraints, anti-predatory behaviour or searching ability are more influential requires further research. However, it is clear that commonly used functional response models are often inappropriate for granivorous birds, and most likely for many other forager types too (Holling 1959; Hassell *et al.* 1977; Jeschke *et al.* 2003).

5.6 References

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Chapter 6

Searching mode and attack behaviour of granivorous birds

6.1 Abstract

1. Searching is a fundamental component of foraging for many species and is important for predicting feeding rates and how these are affected by prey density (the functional response). The searching rate is difficult to measure because of the difficulty interpreting perceptual abilities of a forager and how these are affected by foraging conditions.

2. Here we study the searching behaviour of two species of ground feeding granivorous birds (grey partridge and chaffinch) to address two fundamental questions: (1) Do these species forage in a continuous mode or a pause-travel mode? And (2) Do these species detect prey equally across their wide visual field? Both these questions relate to the area searched over time and, thus, both have implications for predicting the functional response.

3. Here I showed that both these species predominantly use a foraging mode akin to pause-travel in unobstructed habitat at seed densities ranging from 5 to 50 seeds m^{-2}, but the proportion of searching bouts containing movement increased in a stubble treatment, thus showing greater continuous foraging behaviour.

4. Additionally, I found that whilst the visual field of these foragers is wide they preferentially target prey in the frontal zone (forward 90^o projection)

over those in the peripheral zones, yet they attack prey over similar distances (mean and maximum) in both zones. Consequently, the searching area is probably over-estimated when assuming either foraging mode because most searching models assume equal search effort over the entire visual field.

5. Although the functional response of grey partridge was predicted better using the holling's disc model and a searching model that assumes continuous searching rather than pause-travel it is likely that simplifying assumptions in both models cause an overestimation of the searching rate.

6. I have shown that the foraging mode of these species is dependent on the prey abundance and availability, but under the conditions used in most foraging experiments (high prey density, visible prey) a pause-travel mode predominates. Accurately quantifying the searching rate is vital for predicting the functional response and these results show that many assumptions about searching behaviour are erroneous, and more exploration of searching behaviour is required.

6.2 Introduction

The functional response, i.e. the feeding rate as a function of prey density, is a central concept in ecology describing the interactions between trophic levels and linking resource abundance to population level demographics. The type II functional response is common to a variety of taxa (i.e. Hassel, Lawton & Beddington 1977; Goss-Custard *et al.* 2006; Nilsen *et al.* 2009; Baker *et al.* 2010) and describes an inverse hyperbolic function where the intake rate increases at a decelerating rate with prey density. The functional response has been described mechanistically as a function of time spent searching for prey and the time spent handling prey. The predator is searching-limited at low prey densities, with the slope at origin equal to the searching rate (Jeschke *et al.* 2002), but as the prey density increases the time spent searching decreases until prey handling becomes the dominant behavioural state and begins to limit the feeding rate. Thus, the searching rate is crucial in determining the rate at which the asymptote is approached and the degree to which prey density affects feeding rate.

For ground feeding birds that detect prey visually two broadly defined searching strategies have emerged: (1) a pause-travel foraging mode in which the bird scans the surface whilst stationary (pause) before either attacking a detected prey or moving to a new pause location; and (2) a continuous foraging mode in which the bird scans the surface whilst in motion. The former is observed commonly in ground feeding birds when foraging for invertebrates, i.e. blackbirds *Turdus merula* L (Poole *et al.* 2007), grey plover *Pluvialis squatarola* L (Pienkowski 1982) and lapwing *Vanellus vanellus* L (Butler & Gillings 2004). Here pause-travel is an advantage because many invertebrate prey respond defensively upon detection of a predator and this tactic reduces the chance of detection. Additionally, prey can often be detected better when a predator is stationary which increases the searching efficiency when foraging for cryptic and evasive prey (Stillman, Goss-Custard & Alexander 2000). Continuous foraging is commonly observed in birds that search for prey that are unresponsive to the presence of the forager, such as seeds (i.e. Smart *et al.* 2008) and grass (i.e. Spalinger & Hobbs 1992; Durant *et al.* 2003). However, even for birds that exhibit a continuous foraging mode when prey availability is low behaviour akin to pause-travel foraging might be used when prey is easily detectable, as here movement is unnecessary for detection and is energetically costly. Andersson (1981) suggests that the choice of foraging mode depends on the relative energy expenditure of each mode versus the expected energetic gain from prey capture. Thus, the foraging mode might be dependent on the abundance, distribution and detectability of prey (Andersson 1981), and whilst a forager may have evolved characteristics that benefit one mode over another (Martin 2007; Fernandez-Juricic *et al.* 2008) these advantages are likely to be dependent on the foraging conditions.

This is important because deterministic models used to calculate the feeding rate differ between pause-travel and continuous foragers and will produce different estimates of searching rate. Prey densities used in most functional response experiments are high enough that the nearest-neighbour distance between prey is usually far less than the perceptual range of the forager (i.e. Robinson 1997; Smart *et al.* 2008; Baker *et al.* 2009). Thus, a new prey item may be detected without moving from the location of the previously captured prey item and the attack will be initiated from this position. Whilst prey densities have tended to be too high in such experiments to necessitate active searching, several studies have used cryptic prey/background combinations which can reduce prey detec-

tion (Getty & Pulliam 1993; Jones, Krebs & Whittingham 2006). Whittingham & Markland (2002) found the birds spent more time searching in grass substrate than bare soil and covered a greater amount of ground when prey density was lowest. Because the study was not focused on searching mode the authors do not report the number of paces per searching bout and, thus, the number of bouts where no movement was required (pause-travel) is not reported.

In this study we examine the foraging mode of granivorous birds, which is somewhat ambiguous having been defined as both continuous (Smart *et al.* 2008; Baker *et al.* 2009; Baker *et al.* 2010) and pause-travel (Getty & Pulliam 1993). We predict that the observed foraging behaviour will resemble that of pause-travel foragers when the distance between neighbouring prey items is less than the maximum attack distance. Here attacks will occur from a stationary position and searching movement will be minimal. We predict that more active foraging will be necessary in obstructed habitats as the detection distances will be shorter (Baker *et al.* 2009). We also quantify the searching effort over the full range of the bird's visual field as a previous study (Poole *et al.* 2007) showed that assuming a circular searching area over-estimates the searching area of a pause travel forager. Here we quantify the distribution of predation events between the frontal and peripheral regions of the bird's visual field and compare the attack distances between these regions. Lastly, we test the assumption (see Chapter 5) that the birds target the closest prey item with greatest frequency when foraging. We discuss these results in the context of estimating the searching rate of foragers in functional response models where ambiguity in this parameter can have a large effect on the predicted functional response (Stephens *et al.* 2003).

6.3 Methods

6.3.1 Behavioural experiments

We used data from two separate experiments to study the searching behaviour and the distribution of attack distances, both experiments have been published previously (Baker *et al.* 2009; Baker *et al.* 2010). These studies require substantial reanalysis of the raw video files to answer the questions posed here. Two study species were used in this analysis, grey partridge *Perdix perdix* L, a large granivorous non-passerine (~390 g) and chaffinch *Fringilla coelebs* L,

a small (~25 g) granivorous passerine. For a full description of these experiments refer to the relevant publications (chaffinch (Baker *et al.* 2009); grey partridge (Baker *et al.* 2010)), but a brief overview will be given here. The chaffinch foraging experiments were conducted at the RSPB Nature Reserve Arne, Dorset, UK. Three purpose-built feeding platforms were used to mimic the natural foraging environment of the birds: bare soil, low density stubble (60 stems m^{-2}) and high density stubble (120 stems m^{-2}). A photographic hide (www.wildlifewatchingsupplies.com, medium dome hide) was set up 4 m from the front edge of the platform and from the hide the birds were filmed using a Canon XL1 video camera mounted on a tripod and set to a height of 1 m above the platform. Rapeseed was used throughout the study and the foraging experiments conducted at seed densities of 25, 50, 100, 200, 400, 800 and 1600 seeds m^{-2}, although only the lowest two densities were analysed for attack distance . In order to minimise the effect of depletion at the lower three seed densities several were conducted (n = 5 or 6 for 25 & 50 seeds m^{-2}, n = 4 for 100 seeds m^{-2}) and only the first few birds to feed in each trial were considered in the analysis. The experiments were conducted between 28 January 2008 and 12 February 2008, in the following order: low density stubble, bare soil, and high density stubble. The first trial would begin at 09:00 h and were stopped by 16:30 h when the light levels were too low to obtain good video footage. At the beginning of each trial, a randomly-allocated seed density would be spread out on the platform and filming would begin. The trial would continue until at least five birds had consumed a minimum of five seeds each at the densities above 200 seeds m^{-2}, and at least three birds had consumed five seeds each at the lower densities. The minimum interval between trials was maintained at 10 minutes throughout in order to reduce the disturbance to the birds.

Grey partridge experiment was conducted on the rearing fields at the Game & Wildlife Conservation Trust, Fordingbridge, Hampshire, in southern England. Five groups of five birds were housed in separate 3 x 6 m pens divided centrally into two 3 x 3 m pens connected via a small hatch (see Baker *et al.* 2010 for full details of housing and animal husbandry). A 1.5 m^2 experimental platform, built from three 1 x 0.5 m plywood boards attached to a wooden frame, was placed centrally in each of the front pens. The stubble platforms were constructed similarly, but with the addition of stubble stems glued in place. Eight different seed densities (5, 10, 15, 25, 50, 100, 200, 400 seeds m^{-2}) were used in the origi-

nal experiment to measure the full functional response, although only the lowest three densities are analysed in this present study. We used one replicate per group of birds for each of the seed densities above 25 seeds m^{-2}, but several replicates were required to film all the individual birds foraging at the lower densities. This was repeated for both the bare soil and stubble treatments. The food was removed from each pen at 08:30 and the first experiment starting at 09.30. There was a one hour interval between each experiment throughout the study in order to maintain a consistent level of hunger. Four replicates were conducted on each pen per day, with each replicate taking not more than four minutes. The seed densities and treatments were fully randomised for each group throughout, but in order to maintain even spacing between the replicates the group order was randomly chosen anew each day. Pre-sieved soil was spread evenly across the platform and the appropriate number of wheat seeds were randomly scattered. The birds were filmed from a Canon XL1 video camera placed 1.5 m from the front edge of the platform (outside of the pen) and at a height of 1 m above the platform. Filming was started immediately upon set up and continued until each bird had made six or more (three or more at < 25 seeds m^{-2}) consecutive pecks or until significant depletion of seeds had occurred across the whole platform. At all densities we were careful to focus on foraging bouts that occurred on previously unused portions of the platform so that depletion would not affect the observed feeding rate.

6.3.2 Analysis of behavioural experiments

For each predation event (i.e. peck) the number of paces taken by the focal individual from the position of the previous predation event until the initiation of the next attack was recorded; thus, the first predation event of a feeding bout is excluded. The distribution of attack distance between the different portions of the bird's visual field was determined by dividing the bird's visual field into four equal wedges representing frontal partially binocular vision, lateral monocular vision and the blinded section at the rear (Fernandez-Juricic *et al.* 2008) (see Fig. 2). Throughout this study these will be referred to as zones 1 (frontal) and zone 2 (lateral) and no distinction will be made between the right and left lateral zones, but this was accounted for in the analysis where appropriate. For each attack the angle from the bird's body posture prior to the initiation of attack, i.e. the last moment of detection, to the target seed was categorised into a zone 1 or

zone 2 detection event. The mean attack distance was calculated as the mean of all birds within a particular treatment and the maximum attack distance was calculated as the mean of the maximum attack distance for each bird. In the initial analysis of both these experiments the attack distance was measured for each observed attack. Here the attack distance is defined as the distance between the birds position at the initiation of attack (measured from between its feet) to the targeted prey item. The attack distances were measured using slightly different techniques between Baker *et al.* (2009) and the subsequent grey partridge studies, however, both techniques were shown to have a similar error (Baker *et al.* (2009) ± 3.3%; Baker *et al.*. (2010) ± 3.1%) and the technique adopted for the latter studies just increases the efficiency. For the chaffinches the distances were measured using a purpose built grid placed on the computer monitor, which allowed the 2-dimensional movements of the birds to be measured. For the grey partridge studies a screen capture of the start and finish positions of the bird was importing into Photoshop CS4 (www.adobe.com). A 15 x 15 cell grid layer was placed over the top of the video images and the grid was warped using the perspective tools to fit over the shape of the platform. In each study the attack distances were measured at only the lowest densities as movement becomes very limited at low prey densities (chaffinch 25 and 50 seeds m^{-2}; grey partridge 5, 10, 15 seeds m^{-2}). The attack distances were measured for each predation event recorded and therefore there was a minimum of three predation events per bird.

6.3.3 Prey targeting experiments and analysis

We tested the prediction that a forager always targets the nearest prey item by measuring the attack distances of grey partridge foraging for wheat seeds on a feeding platform where the location of each seed was known and comparing the attack distance to the distance to the other available seeds. The experiments were conducted on the rearing fields at the Game & Wildlife Conservation Trust, Fordingbridge, Hampshire, in Southern England, using grey partridge purchased at 8-weeks-of-age from Heart of England Farms (Warwickshire, UK). The housing conditions and experimental setup followed that described in Baker *et al.* (in press), although here there were only three groups of six birds. Additionally, the foraging experiments were conducted on two different foraging platforms, a bare soil platform and an uneven platform. The uneven platform was constructed from moulded rubber matting that consisted of raised squares 1.5 cm in height and 6

cm along a side spaced evenly at 3 cm apart, creating a regular pattern of raised and sunken ground over which to forage; this was laid over a 1.5 x 1.5 m plywood frame (as per Baker *et al.* (2010)). The bare soil platform was constructed similarly but using a flat substrate and both substrates were painted green to match the surrounding grass. Because we required birds to forage singly on the platform we added a wooden barrier that led the birds from the housing pen to the feeding platform in the adjacent pen in single file, thus staggering the birds arrival.

The experiments were conducted from the 9th – 13th November 2009 between 10:00 h and 13:00 h. I scattered circular metal washers, 1 cm in diameter, onto the feeding platform at a density of 12 m^{-2} and filmed the location of the washers. Each washer was then replaced with a wheat seed before the birds were allowed into the experimental enclosure and were filmed consuming the seeds. Replicates were repeated in a random order and the treatments were fully randomised throughout until all individuals had been filmed foraging on the platform. The videos were downloaded onto a PC and analysed using purpose built event recording software. The location of each seed on the platform and the distance from the forager to each seed were measured using the method of Baker *et al.* (2010), as described in the preceding section. The distance between the forager and the target seed at the moment of attack initiation was compared with the distance to the remaining seeds on the platform for three to five pecks. Additionally, each attack was categorised into a zone 1 or a zone 2 detection event, as described previously.

6.3.4 Statistical analysis

I used a generalised linear model with a Poisson error distribution to test the effects of prey density and habitat structure (including their interaction) on the number of paces given the observed distribution of the response variable. The model was fitted with the nlme R package (Pinheiro *et al.* 2008). Because the attack distance data was obtained from several different experiments under differing conditions (seed density and habitat structure) I compare the mean and maximum attack distances in each zone within each experiment only. We used a pair t-test to compare the attack distances in zones 1 and 2 for each bird (i.e. observations from zones 1 and 2 from the same foraging bout) so that individual variation in attack distance could be taken into account.

The Holling's disc equation was used to predict the functional response of

	Mean observed values	
	Bare soil (±95 % CI)	Stubble (±95 % CI)
Habitat structure		
Stubble density (stems m^{-2})	0	70
Behavioural parameters		
$H_t(s)$	0.851 (±0.04)	0.851 (±0.04)
Search speed (s)($m\ s^{-1}$)	0.274 (±0.016)	0.274 (±0.016)
Maximum attack distance (d)(m)	0.293 (±0.050)	0.233 (±0.036)
Pause duration (T_p)(s)	0.852 (±0.151)	0.966 (±0.217)
Search rate (a)($m^2 s^{-1}$)		
Continuous ($a = 2ds$)	0.159	0.129
Pause-travel ($a = A/T_p$)	0.237	0.132

Table 6.1: The experimentally measured behavioural parameters used to predict the functional response of grey partridge foraging in bare soil and stubble habitat treatments. Searching rate is calculated assuming either continuous foraging or pause-travel foraging.

grey partridge having been shown previously to provide the best predictions of the observed functional response from experimentally measured behavioural parameters (Baker *et al.* 2010). The searching rate was calculated under the assumption of either pause-travel or continuous foraging. For pause-travel foragers the searching rate was calculated as

$$a = \frac{A_{search}}{T_{search}} \tag{1}$$

where a = the searching rate ($m^2\ s^{-1}$), A_{search} is the area searched during a single pause (m^2) and T_{search} is the time spent in a pause (s) (Poole *et al.* 2007). For continuous foragers the searching rate was calculated as

$$a = 2ds \tag{2}$$

where s = the travel speed during searching ($m\ s^{-1}$) and d = the maximum attack distance (Spalinger & Hobbs 1992; Fortin *et al.* 2004; Smart *et al.* 2008). All the behavioural parameters were measured experimentally (see Table 6.1).

R 2.10.1 (www.R-project.org) was used for all statistial analysis and for the production of all graphs.

6.4 Results

6.4.1 Do these granivorous bird species exhibit continuous or pause-travel behaviour?

As the definition of a continuous forager is one that searches whilst moving (as assumed by the searching models of continuous foragers (Andersson 1981; Spalinger & Hobbs 1992; Stillman & Simmons 2006) we would expect that the greater proportion of searching bouts contain movement. As can be seen from Figure 6.1 most predation events even at these low densities required no movement or only a single pace before an attack was initiated. In the unobstructed bare soil treatments for both species the percentage of searching periods that contained no movement was > 60% at prey densities higher than 10 seeds m^{-2}. For grey partridge both prey density (b = -0.05, z = -4.177, $P < 0.001$) and habitat (b = 0.417, z = 3.905, $P < 0.001$) affected the number of paces. For chaffinches prey density did not affect the number of paces (b = -0.002, z = -0.0466, $P = 0.641$), but both stubble treatments did have a significant affect (stubble (low); b = 1.032, z = 6.045, $P < 0.001$: stubble (high); b = 0.525, z = 3.024, $P = 0.003$). Thus, these foragers exhibit pause-travel type behaviour frequently at the prey densities used in these studies when foraging in unobstructed habitats. Whilst still accounting for a large proportion of the searching bouts the ability to detect prey whilst stationary is reduced in the stubble treatments as predicted.

6.4.2 Do granivorous birds focus their attacks frontally or laterally?

For all attack distance observations a significantly higher percentage of attacks occurred in zone 1 (73.18%) than zone 2 (26.82%) (X^2 = 599.53, df = 1, $P <$ 0.0001) suggesting that the birds are preferentially searching ahead, attacking fewer prey laterally (see Fig. 6.2 for the percentage distribution of attacks for each separate experiment and treatment). The overall percentage of lateral attacks was lower in the stubble treatments (23.02%) than bare soil (33.18%), which is probably due to the visual obstruction caused by the stubble stems. Table 6.2 shows the results of the paired t-tests for the mean and maximum attack distances between zones 1 and 2. With only a few exceptions there was no significant difference between the attack distances in these zones. A significant difference

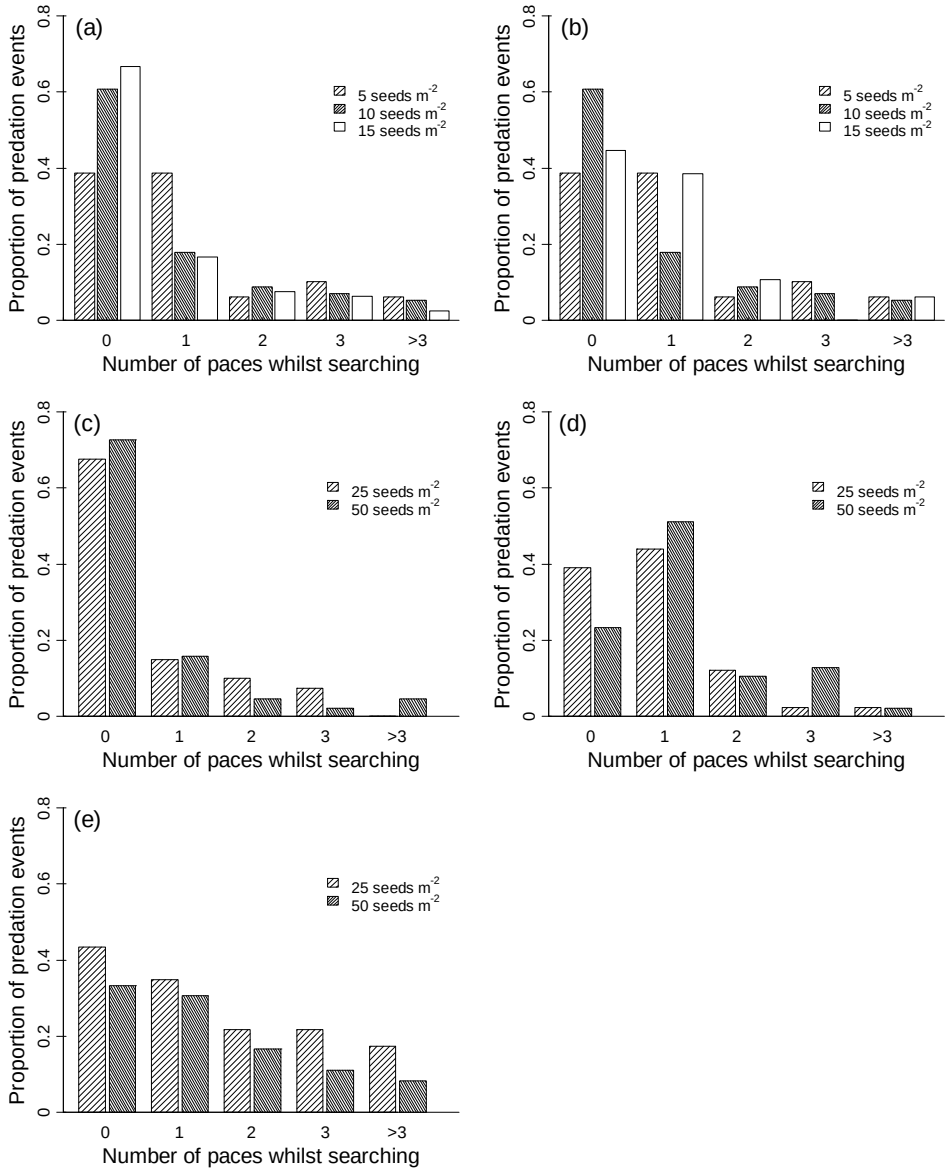


Figure 6.1: Frequency distributions showing the number of paces taken by two species of granivorous birds (grey partridge and chaffinch) whilst searching for seeds (wheat and rapeseed, respectively) in bare soil and stubble habitats at several low seed densities: (a) grey partridge bare soil treatment; (b) grey partridge stubble treatment; (c) chaffinch bare soil treatment; (d) chaffinch low density stubble treatment; and (e) chaffinch high density stubble treatment.

was found for both the attack distances in the bare soil treatment at 5 and 10 seeds m^{-2} and the maximum detection distance for grey partridge at 5 seeds m^{-2}.

6.4.3 Do granivorous birds preferentially target the closest prey?

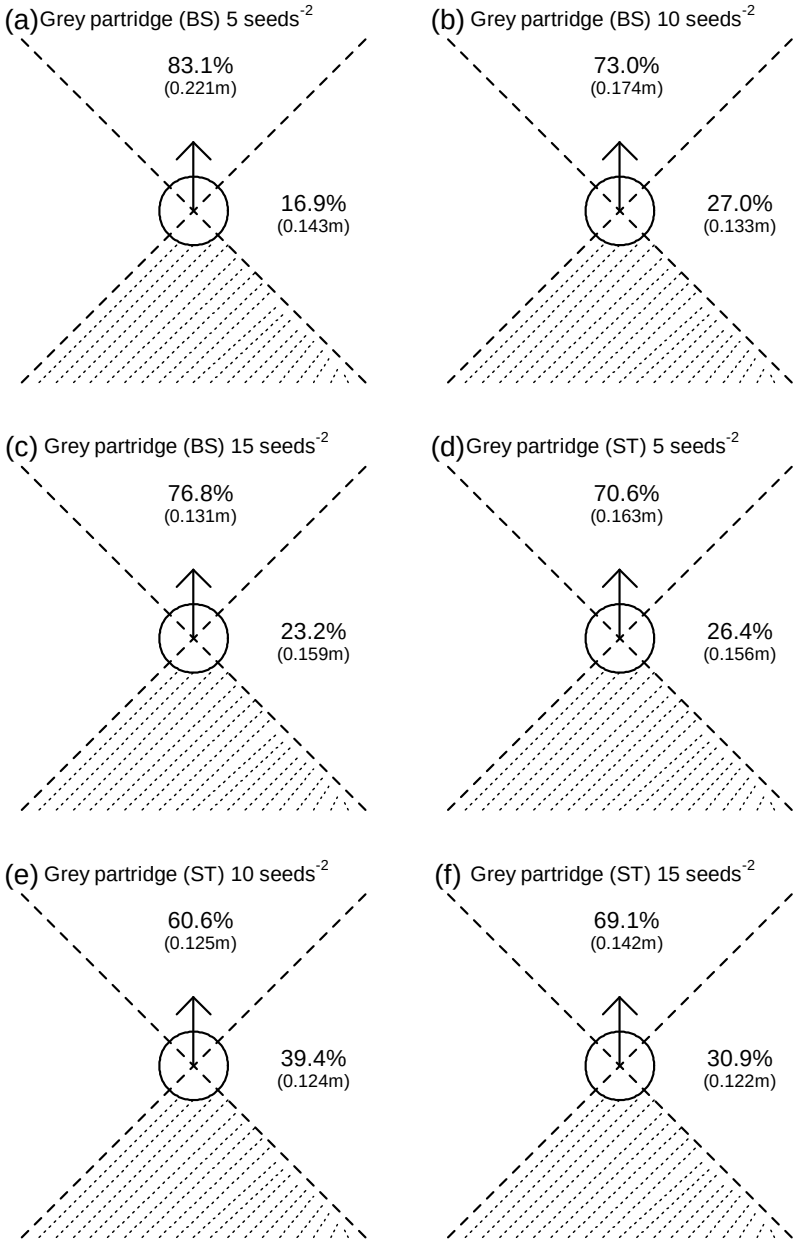
We found that a significantly higher proportion of the nearest prey items were targeted during a foraging bout than the next nearest item in the flat treatment ($X^2 = 10.37$, $df = 1$, $P = 0.0013$), but not in the uneven treatment ($X^2 = 1.28$, $df = 1$, $P = 0.258$). In total 55.2% (flat) and 48.3% (uneven) of prey items consumed were the closest prey item at the moment of detection and the closest two prey accounted for 76.1% (flat) and 83.3% (uneven) of predation events (Fig. 6.3). Additionally, I tested whether consumption of the second closest prey item in preference to the closest item occurs at a higher than expected frequency in the frontal visual zone (1). This would again show that the foragers preferentially focus on this frontal region when searching and suggest that detection in the lateral zones is poorer. I found a significant difference between the two zones in both treatments, bare soil ($X^2 = 111$, $df = 1$, $P < 0.001$) and uneven ($X^2 = 28.38$, $df = 1$, $P < 0.001$).

6.4.4 Predicting the functional response

To compare the effect of estimating searching rate assuming either a continuous or a pause-travel foraging mode, I predicted the functional response of grey partridge (Baker *et al.* 2010), the most complete functional responses measured for granivorous foragers, using experimentally measured behaviour parameters (Table 1). The parameter of pause time was measured for each searching bout that contained no movement and excluded any vigilance behaviour. For both bare soil and stubble treatments the search rate calculated assuming a pause-travel (equation 1) foraging mode was higher, although only marginally in the stubble treatment, compared with the continuous (equation 2) foraging mode and this produced a poorer fit to the observed data (Fig. 6.4) (Bare soil, continuous R^2 = 0.311; pause-travel $R^2 = 0.191$: Stubble, continuous $R^2 = 0.150$; pause-travel R^2 = 0.144).

Species	Habitat	Density (seeds m^{-2})	Mean attack distance between attack zones (paired t-test)			Max. attack distance between attack zones (paired t-test)		
			t	df	P	t	df	p
Grey partridge	Bare soil	5	4.310	7	0.004	3.903	7	0.006
		10	1.696	13	0.114	3.418	13	0.005
		15	1.700	13	0.114	2.219	13	0.045
Grey partridge	Stubble	5	1.403	12	0.186	1.859	12	0.088
		10	0.278	14	0.785	0.456	14	0.655
		15	0.741	12	0.473	2.127	12	0.055
Chaffinch	Bare soil	25	-0.218	9	0.832	0.374	9	0.717
		50	-2.324	6	0.059	-1.055	6	0.332
Chaffinch	Stubble - low density	25	0.251	7	0.809	1.217	7	0.263
		50	-0.485	12	0.637	0.117	12	0.909
Chaffinch	Stubble - high density	25	-1.793	5	0.133	0.407	5	0.701
		50	-1.568	8	0.156	-0.563	8	0.589

Table 6.2: Paired t-test results for the mean and maximum attack distances between search zones (zone 1 = frontal 90^o section, zone 2 = lateral 90^o sections) for each of the experiment / treatments.


(a) Grey partridge (BS) 5 seeds-2
83.1%
(0.221m)
16.9%
(0.143m)
(b) Grey partridge (BS) 10 seeds-2
73.0%
(0.174m)
27.0%
(0.133m)
(c) Grey partridge (BS) 15 seeds-2
76.8%
(0.131m)
23.2%
(0.159m)
(d) Grey partridge (ST) 5 seeds-2
70.6%
(0.163m)
26.4%
(0.156m)
(e) Grey partridge (ST) 10 seeds-2
60.6%
(0.125m)
39.4%
(0.124m)
(f) Grey partridge (ST) 15 seeds-2
69.1%
(0.142m)
30.9%
(0.122m)

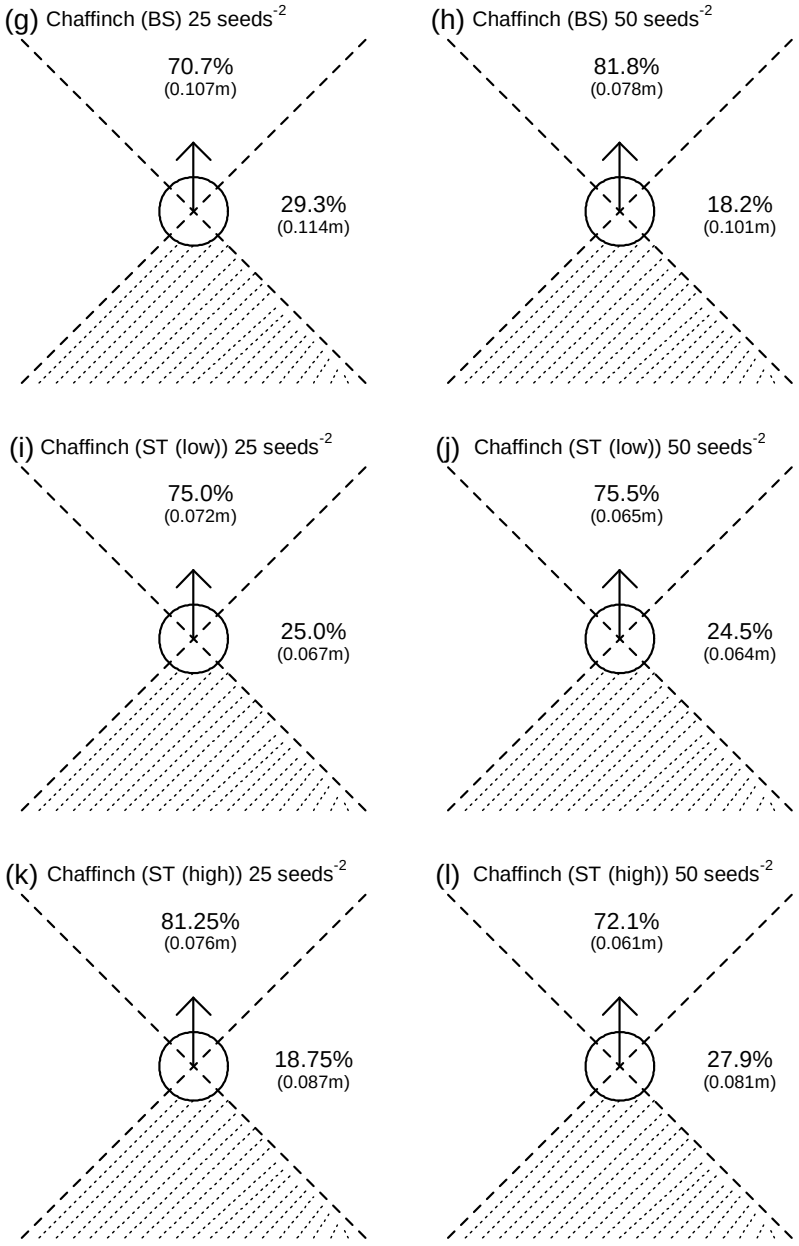


Figure 6.2: The distribution of attack distances between searching zones 1 (frontal – top of diagram) and 2 (lateral – right and left) for grey partridge and chaffinch foraging in several different habitat structures at low seed densities (see individual graph labels for details). No distinction was made between right and left sided attacks and so this data is combined and only one percentage figure is given in the diagram. The numbers in parentheses are the mean attack distances for each detection zone. The hatched area to the bottom on each figure is the visual blind spot to the rear of each forager's central axis (indicated by the arrow).

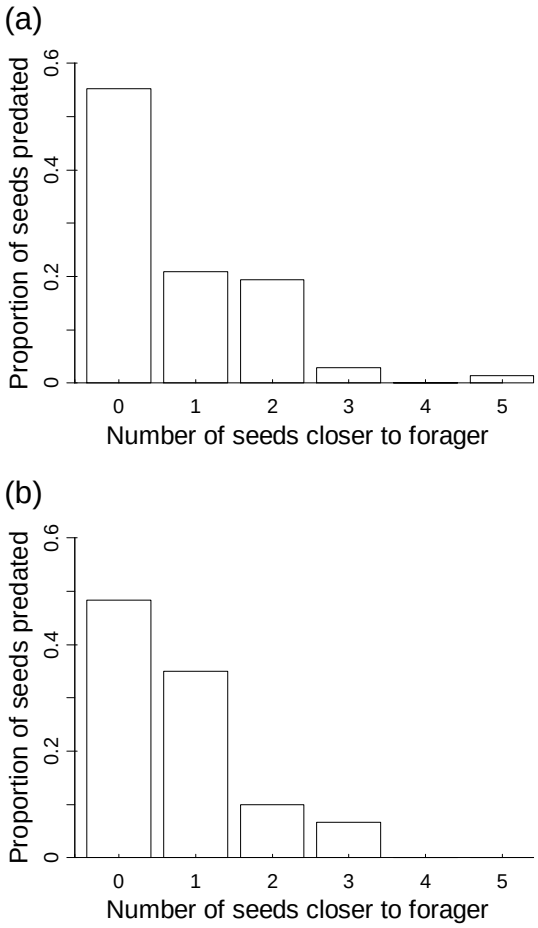


Figure 6.3: The number of seeds closer to the forager during a handling event for grey partridge foraging for wheat seeds of known location, on (a) flat and (b) uneven foraging surfaces. The graphs shows the proportion of predation events where the seed predated was the closest seed to the forager at the point of detection (0) or the proportion of times there were 1-5 seeds closer than the seed targeted.

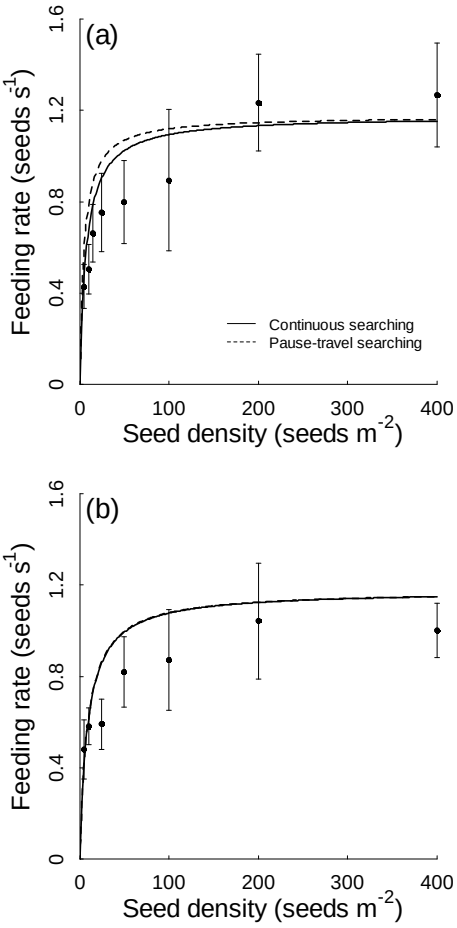


Figure 6.4: The observed functional responses (± 95% CI) of grey partridge in (a) bare soil and (b) stubble habitats. The two lines are the functional response curves predicted using the Holling's disc model and experimentally measured behavioural parameters (Table 2). The R^2 values show that the continuous foraging model (equation 2) explained more variation in the observed functional response. In the stubble treatment the estimates of searching rate using produce similar model fits and therefore the two curves cannot be distiguished.

6.5 Discussion

In this study I have shown that two species of ground feeding granivorous birds behave effectively as pause-travel foragers when prey density is high enough that prey can be detected without moving. This study highlights the false dichotomy of the labels 'continuous' and 'pause-travel' for many foragers where the observed mode of foraging is affected by the abundance, distribution and detectability of the prey. Thus, estimating the searching rate using a model that assumes either continuous or pause-travel searching under all conditions may produce poor estimates as the behavioural mode may switch as the availability of prey changes. Predicting the functional response of grey partridge using a searching rate calculated assuming a pause-travel searching mode produce a similar fit to a continuous searching model in the stubble treatment but a worse fit in the bare soil treatment (Fig. 6.4). However, the simplifying assumptions in the two models of searching rate (equations 1 and 2), i.e. uniform probability of detection with distance and through the complete visual field, are likely to cause an overestimation of the searching rate in both models. Habitat structure that affects the visual detection of prey was shown to increase the number of searching bouts that required movement, which results from the reduced detection distances (Baker *et al.* 2009) and consequently reduces the number of prey that can be detected from a single position. Prey density affected the number of paces in the grey partridge treatments and it appears that at 5 seeds m^{-2} the prey density is causing an increase in the number of searching bouts that require movement. Further studies at lower densities would be needed to confirm the hypothesis that the threshold density for requiring continuous foraging is found when the expected nearest-neighbour distance is greater than the maximum attack distance.

I have shown that two granivorous bird species preferentially target prey in the frontal visual zone and that this preference increases when their visual field was restricted due to the presence of crop stubble, a common foraging habitat for such species. However, I found no difference in the mean or maximum attack distances between attacks aimed at prey directly ahead (zone 1) or attacks aimed laterally (zone 2) suggesting that their ability to detect prey does not differ significantly between the frontal and lateral regions. Poole *et al.* (2007) found that the search area of blackbirds, which forage in a pause-travel mode, was oval in shape with the birds attacking prey over greater distances in the forward direction

than to either side. The observed functional response was predicted most accurately using the 80th percentile of attack distances, suggesting that the previously used method of assuming a circular searching area (minus a wedge representing the blind spot) over-estimates the searching area and therefore the prey encounter rate of these species. However, the 80th percentile attack distance used here produced a far worse fit to the observed functional response data (data not shown). We found a significant difference only in the distribution of predation events between these zones and not the attack distances. This suggest that these species are better adapted to foraging with their eyes converged, and this might be advantageous when using a continuous foraging mode as they can search and navigate simultaneously.

Whether birds detect the same number of prey in their lateral visual field and yet preferentially target prey in their frontal zone is not known. Targeting prey on their periphery will require a change in body posture and direction that could reduce foraging efficiency and searching rate and, therefore, it might be preferable to forgo a closer item on the periphery for a more distance prey lying ahead. Fernandez-Juricic *et al.* (2008) showed that the degree of eye movement in two passerine species allows them to switch between different visual fields, either including a wide area of binocular vision (~46^o in these species) or sacrificing binocular vision for a wide peripheral field. This could explain the observed differences in the frequency of attacks between the frontal and peripheral zones and might suggest that when focusing forward with the visual fields converged to their fullest extent that birds detect prey sub-optimally in the lateral regions, despite their visual field encompassing a wide angle. I have shown that the birds target the closest prey item a significantly greater proportion of the time than the next nearest item on a flat substrate, but on the uneven substrate where visibility was often obscured there was no significant difference in the predation frequency of the closest two prey items. However, in both treatments the closest two prey items accounted for the vast majority of the prey items taken, indicating a clear preference for attacking the nearest prey. The failure to detect the closest prey was more frequent in the lateral zones and, therefore, their lateral detection appears to be sacrificed when using a converged visual field.

Quantifying the searching rate is important for predicting the functional response as the searching rate is a fundamental component of most functional response models (Holling 1959). Here we have shown that the searching behaviour

of two granivorous bird species more closely resembles that of a pause-travel forager at prey densities used in experimental trials. Thus, the foraging mode of these species is dependent on the prey availability (including detectability and abundance) and environmental conditions. Searching occurs to a greater extent in the frontal zone suggesting the assumption of a circular searching area (minus the 90^o wedge at the rear) might over estimate the search area, as shown previously in Poole *et al.* (2007). Although the foraging conditions in these experiments allowed for easy prey detection the prey densities used here were much lower than birds have been observed to forage on in the wild (Moorcroft *et al.* 2002) and, therefore, these findings might translate to wild birds where prey detectability is lower but prey more abundant.

Of all the foraging behaviours commonly included in functional response models quantifying the searching rate is the most challenging. Whilst several complex models have been derived (Andersson 1981; Getty & Pulliam 1991) most of the model parameters remain unquantified and, thus, we are restricted to simple models of searching rate when testing functional response models using empirical data. Through careful experimental study the effect physical and environmental factors on prey detectability and the encounter rate (searching rate $\times$ prey density) should be quantifiable leading to better estimates of the searching rate.

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Chapter 7

Overall discussion

7.1 Mechanistic models of the functional response

Throughout this thesis I have explored the ability of mechanistic functional response models to predict the observed functional responses of several species of granivorous bird by applying the 'experimental component analysis' method first proposed by Holling (1963). Only through the careful and thorough analysis of the model's behavioural parameters can we understand the processes and interactions that affect feeding rate and shape the overall functional response. I have explored the effects of habitat structure on the functional response to determine the mechanism through which feeding rate is reduced in structurally complex foraging environments. I have carefully considered the properties of handling time and divided this component into functionally distinct component processes to try to understand the influence of each component on the observed correlation between handling and prey density. I have explored the properties of routine vigilance and how this behavioural state could interact with handling and searching behaviours to reduce the feeding rate. And finally, I have explored the properties of searching behaviour to determine the mode of searching used by these species and whether the focus of searching is distributed evenly across the entire visual field.

This research extends considerably our current knowledge of the functional responses of granivorous birds, and other foragers with similar behaviour, and has generated many more questions regarding the properties and interactions of the behavioural processes that affect the feeding rate of these species. This should in time lead to the development of functional response models that represent the

foraging behaviour in an increasingly realistic manner and in turn yield a better understanding of the behaviour of these species. Some of the advances brought about through this research and key questions stemming from these findings are discussed in the following subsections.

7.1.1 How do behavioural processes interact?

Holling's (1959) original mechanistic functional response model, the 'disc equation', assumes no interaction between the two behavioural processes of searching and handling. However, several behavioural processes are mutually compatible and by allowing these processes to occur simultaneously greater efficiency in foraging can be achieved. Smart *et al.* (2008) explicitly incorporated vigilance into the functional response model and allowed vigilance to overlap with handling so that vigilance incurs no costs (i.e. reduced feeding rate) when the proportion of time vigilant is less than the handling time. In Chapter 3 I extended the models presented in Smart *et al.* (2008) by representing handling time in finer detail, accounting for the incompatibility of some portions of the handling process with vigilance. By allowing vigilance to overlap with the compatible portion of handling only the effect of vigilance is more realistically represented for foragers with such behaviour. The effect of mutually exclusive searching, handling and vigilance can be seen here by setting the proportion of compatible handling to equal zero (or similarly model 2 from Smart *et al.* 2008). With such assumptions the predicted feeding rate is lower across the full range of functional response because vigilance must be accommodated in addition to searching and handling and the foraging time is increased proportionally.

Here searching and handling were considered mutually exclusive, assuming that any spare time during handling is devoted to vigilance. However, in Chapter 4 I showed that searching overlaps considerably with handling, with searching and vigilance alternating in short burst. A modification to model 2 from Baker *et al.* (2010) could allow searching and vigilance to occur during handling to more realistically represent these behavioural interactions, although several previous models that include such overlaps tended to over-estimate the rate at which the feeding rate approaches the asymptote (Smart *et al.* 2008). However, in addition to searching during handling I found that significant time was spent in a head-down searching posture once handling had finished even when prey was superabundant and, therefore, a time-cost would be incurred, seemingly unneces-

sarily. I ascribed this head-down behaviour to selective searching, i.e. choosing the best food morsels. This extra searching component is not currently included in any functional response model and must be understood if the interaction between handling, searching and vigilance is to be modelled realistically. If searching and vigilance are allowed to overlap without including selective searching behaviour then the feeding rate will be overestimated as it approaches its asymptote.

Many of these scenarios might only be important when foragers are not experiencing time constraints because under time pressure vigilance and selective searching are likely to be sacrificed to increase intake rate (Van Der Veen 2000). However, in such circumstances handling and searching are still likely to be compatible, therefore deviating from the assumptions of the Holling's disc model. Thus, it appears important to study the functional response of foragers under time constraints if we are to understand the fundamental mechanistic processes and interactions that lead to the observed functional response.

7.1.2 Is vigilance a necessary component of the functional response?

Given the comments of the preceding section, when is vigilance a necessary component of functional response models? Routine vigilance was incorporated into functional response models in Chapters 3 & 4, the former allowed vigilance to occur entirely during compatible handling time and the latter distributes vigilance uniformly between handling and searching. However, it is likely that routine vigilance will be sacrificed to maximise intake rate when there are time constraints on foraging and the starvation risk is high (Poysa 1987; Tchabovsky *et al.* 2001). Therefore, under stringent conditions when intake rate might fail to reach the minimum daily energy requirement, routine vigilance might be unimportant in the functional response model. Such stringent conditions will be rare occurrences as animals are often well adapted to avoiding time constraints during average conditions (Wilson 1975). However, vigilance will be an important component of the functional response when predation risk is included, either related directly to the level of vigilance or linked to a patch, because it will affect the probability of survival and the distribution between patches (Robinson 1997; Brown 1999; Cresswell 2008).

Previously, spatial depletion models have incorporated the effect of preda-

tion risk into the model in a probabilistic manner, giving a fixed probability of predation in a patch at each time interval (Robinson 1997; Brown 1999). However, predation risk can have indirect effects on the fitness of a forager (Cresswell 2008), by increasing the time spent vigilant and effecting patch choice, both of which might cause a decrease in daily intake rate (Poysa 1987; Cowlishaw 1997). By incorporating vigilance directly into the functional response model the impact of these indirect effects can be explored through the interaction of increased vigilance on feeding rate. Cresswell (2008) reviewing the non-lethal effects of predation-risk concluded that these effects are best measured through the foraging-predation risk trade-off. Thus, the models developed in this thesis have application beyond simple predictions of intake rate and could provide a key linkage between resource abundance, predation risk and feeding rate.

7.1.2.1 A note on measuring vigilance

Throughout this thesis I have tried to quantify the proportion of time a forager spends vigilant in order to predict the impact of this behaviour on the functional response. In order to do this I chose to define routine vigilance behaviour as the time spent with the head in an upright posture with the bill parallel to the ground or at a greater angle. However, this definition is largely taken for practical reasons because it is possible to observe and quantify this behaviour during video analysis. Whilst this posture is likely to signal routine vigilance, several studies have shown that predator detection still occurs in head-down postures, a position that has been defined here as non-vigilant. For example, Lima & Bednekoff (1999) showed that dark-eyed juncos *Junco hyemalis* L were still able to detect a simulated predator with their head-down, although over a shorter distance. Bednekoff & Lima (2005) found that these birds preferred to forage in a habitat where their visual field was not obstructed when in a head-down position. However, it is clear that head-up vigilance is the optimum posture for detecting predators as foragers tend to increase the amount of head-up scanning in response to higher predation risk or reduced detection potential (Elgar 1989; Whittingham *et al.* 2004; Quinn *et al.* 2006). Therefore, head-up time is probably the best indicator of the perceived threat and is a good metric of the time-costs incurred by engaging in routine vigilance.

7.1.3 How can searching behaviour be further explored?

The searching rate is a difficult parameter to measure as it requires an estimate of the perceptual limits of the forager, and these are often sensitive to physical and environmental conditions, i.e. light intensity, prey crypticity and habitat structure. In Chapter 2 I showed that the functional response is significantly affected by the presence of crop stubble and that the observed decrease in feeding rate was caused by a reduction in the maximum attack distance; effectively reducing the area searched per time and thus reducing the prey encounter rate. In Chapter 6 I showed that our assumption that these species forage using a pause-travel mode is often untrue at even quite high prey densities when randomly distributed prey can be detected without moving. However, using experimentally measured behavioural parameters the functional response is predicted better when a continuous foraging model is used, rather than a pause-travel model. I also showed that attacks were not distributed evenly between the frontal 90^o zone and the two lateral zones, with a much larger proportion of attacks occurring in the former. Neither of the models used here to predict the searching rate account for such uneven distribution of searching effort and, therefore, it is likely that both models over-estimate the searching rate of these foragers.

Whilst the searching rate is under-explored in a mechanistic context, the process of searching should be relatively easy to explore with the appropriate experimental methods. Ioannou, Ruxton & Krause (2008) showed that the encounter rate was not directly proportional to the prey density using fish swimming through a ring of interconnected cells, thus the fish searched over unexplored patches in this effectively one-dimensional arena. Mols *et al.* (2004) allowed caterpillars to move naturally into position on small trees, finding their own protective shelter, before measuring the encounter rate of great tits *Parus major* L, thus simulating natural distributions of prey. For granivorous species more studies must be conducted using complex habitat structure and natural substrates, such as compacted soil and uneven surfaces. Baker *et al.* (2010) used loose soil as the foraging substrate to try and mimic natural substrates. Although this allowed the seeds to sit in the substrate rather than resting above, the wheat seeds were not buried and their straw-yellow colour contrasted with the light brown colour of the soil making detection relatively easy. Several studies have decreased the contrast of seeds with substrate and found significant effects on searching and encounter rates (Getty & Pulliam 1993; Whittingham & Markland 2001; Jones *et al.* 2006).

Complex functions for predicting the instantaneous probability of detection for both pause-travel and continuous foragers have been derived (Andersson 1981, Getty & Pulliam 1991), however, such models include parameters that are difficult to quantify and often not mechanistically defined, i.e. the K parameter in Getty & Pulliam (1991) includes all physical factors that could affect detection. Previously these parameters have been estimated statistically from the observed detection rates; however, this provides no clear insight into the mechanistic functions of these parameters nor provides a true test of the models predictive ability. It is likely that incorporating a distance decay parameters might be useful for estimating the searching rate of these species, however, we must be careful to accurately quantify the distance decay function through experimental study (i.e. Andersson, Wallander & Isaksson 2009) and not through statistical derivation.

7.1.4 Increasing realism: habitat structure, group-size and competition

Throughout this thesis the functional response and the searching behaviour has been measured under different habitat structures with the aim of increasing our understanding of foraging under more natural conditions. Methodologically, increasing the habitat structure can create difficulties by obstructing the experimenters view of the foragers and through replicability of the experimental design. However, replica crop stubbles can be designed to mimic the conditions of those in stubble fields (Butler *et al.* 2005; Baker *et al.* 2009; Baker *et al.* 2010) and because these crops have parallel rows when viewed along the rows a good view of the forager can be obtained. Other authors have used different replica habitats to study foraging behaviour, such as grass substrate (Whittingham & Markland 2002) and cryptic substrates (Getty & Pulliam 1993; Jones *et al.* 2006).

The bare soil conditions used as the null habitat structure in these studies provides an optimum foraging habitat with no visual obstruction, although the contrast of prey against the foraging substrate can reduces detectability and effectively reduces the prey encounter rate (Jones *et al.* 2006). The background colours used here were consistent throughout each study and the prey type the same within each experiment, however, the differences between these experiments mean that I cannot comment on the relative foraging efficiencies between the species. Natural foraging environments are far more complex than the ex-

perimental systems used in these studies and, therefore, the searching efficiency should be expected to be lower than those measured experimentally. Additional complexity in natural systems arises from multiple prey choices, complexity in predation risk (i.e. Jones, Krebs & Whittingham 2007), climatic effects (i.e. Fernandez-Juricic & Tran 2007) and group-size effects (i.e. Beauchamp 2009), including interspecific competition (Johnson, Giraldeau & Grant 2006) and anti-predator effects (Barnard 1980).

I found little effect of habitat structure on vigilance, but previous studies have found that the habitat structure affects patterns and quantity of routine vigilance (Butler *et al.* 2005; Devereux *et al.* 2006). However, the crop stubble used here as the obstructed habitat was designed to provide a foraging obstruction and not specifically an obstruction to anti-predator vigilance. It has been shown elsewhere that the habitat structure can significantly increase routine vigilance and will consequently affect the functional response. Similarly, predation risk from different sources has been shown to change the pattern of routine vigilance and this might affect the functional response (Jones *et al.* 2007).

Additionally, I have found little effect of group-size on the functional response, or any other behaviour process, throughout these studies. A considerable body of research has shown an effect on group-size on routine-vigilance, usually with vigilance showing a negative correlation with group-size (Beauchamp 2009). The absence of an effect might be due to fairly consistent flock sizes throughout the studies, although the time spent vigilant might be set by handling or digestion times which could be independent of group-size. Interspecific competition is usually absent in granivorous farmland birds when foraging in an open field (DJB per. obs.) because prey are handled too rapidly to allow for kleptoparasitism. Where interspecific competition has been observed previously in granivorous birds (Johnson *et al.* 2006) they were foraging at a clumped resource and here it is possible for an individual to guard some of the resources. However, this type of behaviour was only observed occasionally in these studies and was absent at the highest densities.

7.2 The functional response as a tool in conservation

The functional response is undoubtedly an important tool in conservation management when food availability is a limiting factor in population persistence. The functional response can be used to link the available resources to the requirements of current populations and to predict the effects of future scenarios on the demographic trends. However, functional responses must realistically represent the foraging behaviour of the species in question if they are to provide accurate and useful predictions.

The functional responses studied and presented throughout this thesis represent instantaneous functional responses and for these species the instantaneous feeding rate is handling limited at high prey densities. However, Wilson's principle of stringency (Wilson 1975) proposes that species adapt to the times of greatest stringency and, therefore, under average conditions foragers will have no difficulty locating and consuming their daily ration of food. This is illustrated by Figure 7.1 which shows the time spent foraging under average conditions for yellowhammer and linnet (parameters shown in Table 7.1) as calculated by the Holling's disc model rearranged as a function of time (t) and the uniformly distributed vigilance (UDV) model (model 2 from Chapter 4). The daily energy requirements for yellowhammer can be met in only a small fraction of the total time available each day for foraging and, thus, under average conditions these species are not time constrained when foraging . When foraging for the smaller rapeseed (as opposed to wheat) the linnets must consume many more individual seed and thus the foraging time is considerably longer. Whilst the disc model predicts ample foraging time even under stringent conditions for linnets the UDV model predicts that the daily intake rate will not be met under stringent conditions. Thus, only under the severest of conditions will the forager begin to starve and other behavioural and physiological parameters, such as vigilance and digestive limitation (Jeschke *et al.* 2002), could significantly influence when time constraints will begin to affect survival.

For example, heavy snow or frost might reduce the food availability on the ground from high densities to near zero in a short time interval and, in addition to higher energy demands at low temperatures, this will have a particular strong effect on many ground feeding species (Robinson, Baillie & Crick 2007). Un-

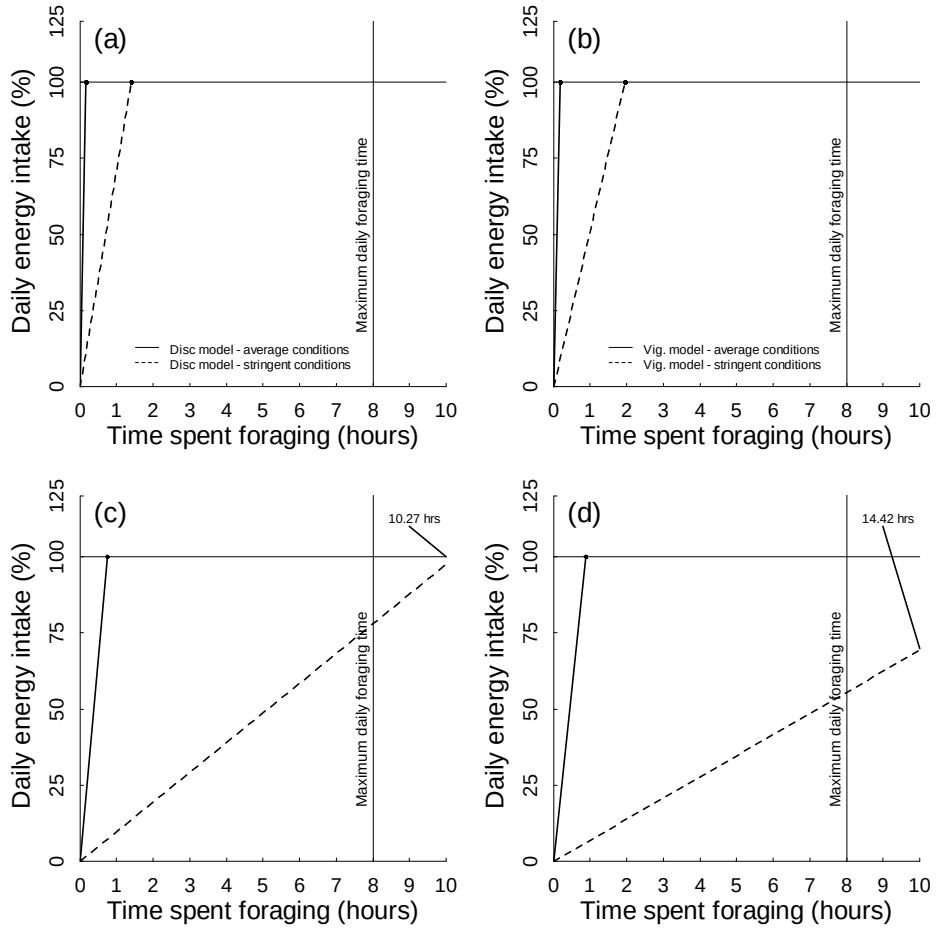

Figure 7.1: Daily foraging time as calculated using the Holling's disc model (Holling 1959) (a & c) and the uniformly distributed vigilance (UDV) model (Chapter 4) (b & d), rearranged as a function of time, under average (-) and stringent (- - -) conditions (see Table 1). a) Yellowhammer (wheat) - Hollings disc model; b) Yellowhammer (wheat) - UDV model; c) Tree sparrow (rapeseed) - Hollings disc model; and d) Tree sparrow (rapeseed) - UDV model.

Parameter	Yellowhammer (wheat)		Tree sparrow (Rapeseed)	
	Initial value	Stringent conditions	Initial value	Stringent conditions
Field metabolic rate (FMR) (KJ day^{-1})	96.28	±25%	83.6	±25%
Body mass (g)	25.89	-	21.04	-
Assimilation efficiency (%)	0.75	0.5	0.75	0.5
Seed mass (g $seed^{-1}$)	0.036	-	0.0027	-
Seed energy density (KJ g^{-1})	15.5	-	23	-
Searching rate (a) (m^2 s^{-1})	0.03	0.003	0.03	0.003
Handling time (H) (s)	2	2	1	1
Seed density (D) (seeds m^{-2})	100	25	100	25
Proportion of compatible H (p)	0.8	0.8	0.8	0.8
Proportion of time vigilant (v)	0.3	0.3	0.3	0.3

Table 7.1: Parameter estimates used to calculate the daily foraging time of yellowhammer and tree sparrows feeding of wheat and rapeseed, respectively. Stringent conditions assume that energetic demands are higher, assimilation efficiency is reduced, seed density is low and that the foraging conditions reduce the searching efficiency. FMR (Nagy 2005), FMR - stringent conditions (i.e. Olson & Kendeigh 1980; Bryant 1997); body mass (BTO bird facts (www.bto.org/birdfacts/)); assimilation efficiency (Brown & Downs 2003); seed mass and seed energy density (Diaz 1990); searching rate (Smart *et al.* 2008; Baker *et al.* 2009); handling times (Chapter 5); seed densities (Moorcroft *et al.* 2002); proportion of compatible handling (Chapters 3 & 4); proportion of time vigilant (Chapters 2 & 4).

der these conditions the birds must rely on their energy reserves and the discovery of unaffected food sources i.e. grain silos, sheltered patches or provisioned food, for survival through this period and the probability of death increases for those weakest individuals in the population. The functional responses presented in this thesis do not account for the encounter rate with new food patches, but assume that the forager is within a patch containing randomly distributed prey and that each prey is consumed in its entirety. Thus, when food availability is suddenly reduced and its distribution becomes patchy and clumped the distribution of these discrete patches and the rate at which these species encounter these remaining resources will be as important as the short-term intake rate. This is where behavioural-based simulation models could be effective as the discovery rate of available patches and the exploitation of those patches based on ideal free distribution and the marginal value theorem could be incorporated based on empirically derived foraging rules. The functional response would be at the heart of such a model, predicting the intake rate, the rate of depletion and ultimately the survival of individuals based on their ability to meet their daily energy demands. More research is required to understand how foragers find and exploit resources under stringent conditions and whether such conditions induce greater competition between individuals over increasingly limited resources, thus favouring dominant individuals.

Therefore, to predict the persistence of granivorous bird populations within agricultural environments using behavioural-based approaches we must study the daily routines, habitat use and availability of resources under stringent conditions when starvation risk is greatest (Nolet & Klaassen 2005). The functional response models developed throughout this thesis have relevance to conservation under stringent conditions so long as the effect of the conditions on the model parameters, especially the density of available prey and the searching rate, are known. Our increased knowledge of the effects of habitat structure and predation risk on the functional response and how to incorporate the effects directly into the models provides a more accurate measure of the feeding rate. This will be especially important in behavioural-based simulation models where foraging decisions are often based on maximising feeding rates and, as I have shown, this is effected by habitat structure and time devoted to incompatible behaviours, such as vigilance.

7.3 Concluding comments

The functional responses developed in this thesis and the behavioural knowledge provided by these detailed studies of the properties and process of each behavioural component of foraging provide an important step towards developing predictive models to link resources abundance to the population level effects in granivorous birds. Whether such models are designed to predict the effects of environmental change on population persistence (i.e. Butler *et al.* 2010) or used to explore theoretical aspects of foraging behaviour, such as the effect of foraging-predation risk trade-off on patch choice (Cresswell 2008), the functional response will often be a key component.

These studies emphasise the importance of the 'experimental component analysis' approach of Holling (1963) whereby an experimental approach is used to parameterise and test the models, rather than deriving parameter estimates statistically. Using this approach I have shown that the foraging behaviour of granivorous birds consistently violates the assumptions of basic mechanistic functional response models and that this can lead to erroneous predictions. It should be possible through careful experimental studies to develop mechanistic functional response models that conform to the observed behavioural characteristics of these species under the full range of naturally occurring foraging conditions.

These studies have highlighted the importance of building strong foundational knowledge of behavioural processes and their interactions if we are to have confidence in the predictions of behavioural-based models. With this strong foundation behavioural-based models can be an important tool in conservation biology and with rapid environmental change exposing populations to previously unobserved conditions this approach may have the greatest potential for extrapolating to these novel conditions.

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Appendix 1

Derivation of functional response with mutually exclusive searching, and partially overlapping handling and vigilance

These models were derived in close collaboration with Richard Stillman.

In order to show similarities with previous models, we derive the function response using the same approach as Smart *et al.* (2008). It is assumed that while searching for food, foragers cannot handle food nor search for predators (i.e. searching for food is mutually exclusive of handling food and vigilance). It is assumed that there are a number of phases to handling food and that searching for predators can only occur during some of these phases (i.e. handling food and vigilance can be partially overlapped). It is assumed that foragers can search for predators while vigilant. Therefore, foragers can occupy four behavioural states, (i) searching for food, (ii) handling food while not vigilant, (iii) vigilant while handling food and (iv) vigilant while not handling food. The total time taken to find and consume a food item is given by

$$T = S + H_H + V_H + V_V \tag{1}$$

where S = time spent searching, H_H = time spent handling while not vigilant, V_H = time spent vigilant while handling and V_V = time spent vigilant while not handling. It is assumed that a maximum proportion of handling time (p) is compatible with vigilance. It is assumed that foragers are preferentially vigilant while handling and attempt to spend all of their vigilance time during the compatible handling time. Therefore, the amount of time vigilant while handling depends on the time spent vigilant (V) and the duration of compatible handling time (pH_t),

where H_t= total handling time. If vigilance time exceeds the compatible handling time, the whole of compatible handling time is spent vigilant. If vigilance time is less than compatible handling time, only this amount of time is spent vigilant while handling.

$$V_H = \begin{cases} pH_t & if\ V \geq pH_t \\ V & if\ V < pH_t \end{cases} \tag{2}$$

The amount of time spent vigilant while not handling is the difference between the total amount of time spent vigilant (V) and the amount of time spent vigilant during handling (equation 2).

$$V_H = \begin{cases} V - pH_t & if\ V \geq pH_t \\ 0 & if\ V < pH_t \end{cases} \tag{3}$$

The amount of time spent handling while not vigilant is the difference between total handling time (H_t) and the amount of time spent vigilant during handling (equation 2).

$$H_H = \begin{cases} H_t - pH_t & if\ V \geq pH_t \\ H - V & if\ V < pH_t \end{cases} \tag{4}$$

Substituting equations 2, 3 and 4 into equation 1 gives

$$T = \begin{cases} S + (H_t - pH_t) + (pH_t) + (V - pH_t) & if\ V \geq pH_t \\ S + (H_t - V) + (V) + (0) & if\ V < pH_t \end{cases} \tag{5}$$

Simplification then gives

$$T = \begin{cases} S + (H_t - pH_t) + V & if\ V \geq pH_t \\ S + H_t & if\ V < pH_t \end{cases} \tag{6}$$

Which can be simplified to

$$T = \begin{cases} S + (1-p)H_t + V & if\ V \geq pH_t \\ S + H_t & if\ V < pH_t \end{cases} \tag{7}$$

It is assumed that the time spent searching is a function of food density

$$S = \frac{1}{aD} \tag{8}$$

where a = searching rate and D = food density. Substituting equation 8 into equation 7 gives

$$T = \begin{cases} \frac{1}{aD} + (1-p)H_t + V & if\ V \geq pH_t \\ \frac{1}{aD} + H_t & if\ V < pH_t \end{cases} \tag{9}$$

It is assumed that foragers spend a constant proportion of the total time vigilant

$$V = vT \tag{10}$$

where v = proportion of time spent vigilant. Substitution of equation 10 into equation 9 gives

$$T = \begin{cases} \frac{1}{aD} + (1-p)H_t + vT & if\ vT \geq pH_t \\ \frac{1}{aD} + H_t & if\ vT < pH_t \end{cases} \tag{11}$$

Which can be rearranged to give

$$T = \begin{cases} \frac{\frac{1}{aD} + (1-p)H_t}{(1-v)} & if\ vT \geq pH_t \\ \frac{1}{aD} + H_t & if\ vT < pH_t \end{cases} \tag{12}$$

Substituting T in the logical comparison with the corresponding formula gives

$$T = \begin{cases} \frac{\frac{1}{aD} + (1-p)H_t}{(1-v)} & if\ v\left(\frac{\frac{1}{aD} + (1-p)H_t}{(1-v)}\right) \geq pH_t \\ \frac{1}{aD} + H_t & if\ v\left(\frac{1}{aD} + H_t\right) < pH_t \end{cases} \tag{13}$$

Which can be rearranged to give

$$T = \begin{cases} \frac{\frac{1}{aD} + (1-p)H_t}{(1-v)} & if\ \frac{1}{D} \geq \frac{(p-v)aH_t}{v} \\ \frac{1}{aD} + H_t & if\ \frac{1}{D} < \frac{(p-v)aH_t}{v} \end{cases} \tag{14}$$

The inequalities are not simplified by taking the reciprocal of both sides as the directions of the resulting inequalities will depend on the sign of $p - v$.
Feeding rate is found from the reciprocal of equation 14

$$F = \begin{cases} \frac{(1-v)}{\frac{1}{aD}+(1-p)H_t} & if\ \frac{1}{D} \geq \frac{(p-v)aH_t}{v} \\ \frac{1}{\frac{1}{aD}+H_t} & if\ \frac{1}{D} < \frac{(p-v)aH_t}{v} \end{cases} \tag{15}$$

Which can be rearranged to give

$$F = \begin{cases} \frac{(1-v)aD}{1+(1-p)aDH_t} & if\ \frac{1}{D} \geq \frac{(p-v)aH_t}{v} \\ \frac{aD}{1+aDH_t} & if\ \frac{1}{D} < \frac{(p-v)aHt}{v} \end{cases} \tag{16}$$

which is the new functional response model (termed model 2 in the text).

The inequality in equation 16 is expressed in a form that is consistent with Smart *et al.* (2008) (i.e. food density on the left side), but note that it can be rearranged to give.

$$F = \begin{cases} \frac{(1-v)aD}{1+(1-p)aDH_t} & if\ v\left(\frac{1}{aD}+H_t\right) \geq pH_t \\ \frac{aD}{1+aDH_t} & if\ v\left(\frac{1}{aD}+H_t\right) < pH_t \end{cases} \tag{17}$$

The term to the left of the inequality is the total time required for vigilance per food item consumed and the term to the right is the total amount of vigilance compatible handling time per food item consumed. This shows that the alternative forms of the functional response correspond to cases in which vigilance either can (bottom form) or cannot (top form) be contained within compatible handling time.

The new model (equation 16) can be reduced to equations 2 or 4 of Smart *et al.* (2008) by changing the value of p. When p = 0 none of handling time is compatible with vigilance (i.e. they are mutually exclusive), as assumed by equation 2 of Smart *et al.* (2008). When p = 1 all of handling time is compatible with vigilance, as assumed by equation 4 of Smart *et al.* (2008).

Setting p = 0 and substitution into equation 16 gives

$$F = \begin{cases} \frac{(1-v)aD}{1+aDH_t} & if\ \frac{1}{D} \geq \frac{-vaH_t}{v} \\ \frac{aD}{1+aDH_t} & if\ \frac{1}{D} < \frac{-vaH_t}{v} \end{cases} \tag{18}$$

Simplification then gives

$$F = \begin{cases} \frac{(1-v)aD}{1+aDH_t} & if\ \frac{1}{D} \geq -aH_t \\ \frac{aD}{1+aDH_t} & if\ \frac{1}{D} < -aH_t \end{cases} \tag{19}$$

Since $\frac{1}{D}$ is always greater than zero, equation 19 can be simplified to

$$F = \frac{(1-v)aD}{1+aDH_t} \tag{20}$$

which is equation 2 of Smart *et al.* (2008).

Setting $p = 1$ and substitution into equation 16 gives

$$F = \begin{cases} (1-v)\,aD & if\ \frac{1}{D} \geq \frac{(1-v)aH_t}{v} \\ \frac{aD}{1+aDH_t} & if\ \frac{1}{D} < \frac{(1-v)aH_t}{v} \end{cases} \tag{21}$$

Taking the reciprocal of the inequality (now possible because both sides are always positive) gives

$$F = \begin{cases} (1-v)\,aD & if\ D \leq \frac{v}{(1-v)aH_t} \\ \frac{aD}{1+aDH_t} & if\ D > \frac{v}{(1-v)aH_t} \end{cases} \tag{22}$$

which is equation 4 of Smart *et al.* (2008).

The inequality in equation 16 can be used to predict the combinations of p and v for which vigilance will limit feeding rate (i.e. when feeding rate is a function of vigilance time). This will occur when

$$\frac{1}{D} \geq \frac{(p-v)aH_t}{v} \tag{23}$$

Which can be rearranged to give

$$p \leq \frac{v(1+aH_tD)}{aH_tD} \tag{24}$$

Appendix 2

Derivation of functional response with mutually exclusive searching, uniformly distributed vigilance and partially overlapping handling and vigilance

These models were derived in close collaboration with Richard Stillman.

In order to show similarities with previous models, we derive the function response using the same approach as Smart *et al.* (2008) and Baker *et al.* (in press). It is assumed that while searching for food, foragers cannot handle food nor be vigilant (i.e. searching for food is mutually exclusive of handling food and vigilance). It is assumed that there are a number of phases to handling food and that vigilance can only occur during some of these phases (i.e. handling is divided into phases that are either compatible or incompatible with vigilance). It is assumed that vigilance is uniformly distributed throughout time (this assumption differs from that used in previous models). Therefore, foragers can occupy four behavioural states, (i) searching for food, (ii) handling food while not vigilant, (iii) vigilant while handling food and (iv) vigilant while not handling food. The total time taken to find and consume a food item is given by

$$T = S + H_H + V_H + V_V \tag{1}$$

where S = time spent searching, H_H = time spent handling while not vigilant, V_H = time spent vigilant while handling and V_V = time spent vigilant while not handling. It is assumed that foragers spend a constant proportion of the total time vigilant

$$V = vT \tag{2}$$

where V = amount of time vigilant and v = proportion of time spent vigilant. The time spent vigilant during handling is found from

$$V_H = vH_c \tag{3}$$

where H_c = duration of handling time compatible with vigilance. The time spent vigilant while not handling is given by the total amount of time vigilant minus the amount of vigilance that occurs during compatible handling

$$V_v = V - V_H. \tag{4}$$

Substituting equations 2 and 3 into equation 4 gives

$$V_v = vT - vH_c \tag{5}$$

The time spent handling while not vigilant is the duration of handling time that is incompatible with vigilance plus the duration of compatible handling during which vigilance does not occur

$$H_H = H_x + (1-v)H_c \tag{6}$$

where H_x = duration of handling time that is incompatible with vigilance. Substituting equations 3, 5 and 6 into equation 1 gives

$$T = S + H_x + (1-v)H_c + vH_c + vT - vH_c \tag{7}$$

Which can be simplified to give

$$T = \frac{S+H_x}{1-v} + H_c. \tag{8}$$

It is assumed that the time spent searching is a function of food density

$$S = \frac{1}{aD} \tag{9}$$

where a = searching rate and D = food density. Substituting equation 9 into equation 8 and rearranging gives

$$T = \frac{1}{(1-v)aD} + \frac{H_x}{1-v} + H_c. \tag{10}$$

Feeding rate is found from the reciprocal of equation 10 to give

$$F = \frac{1}{\frac{1}{(1-v)aD} + \frac{H_x}{1-v} + H_c} \tag{11}$$

where F = feeding rate. Which can be rearranged to give

$$F = \frac{(1-v)aD}{1+aD(H_x+(1-v)H_c)}. \tag{12}$$

Which is termed Model 1 in the text.

Equation 12 can be further simplified by assuming that compatible and incompatible handling times are a fixed proportion of total handling time (H_t)

$$H_c = pH_t \tag{13}$$

$$H_x = (1-p)H_t \tag{14}$$

where p = proportion of handling time that is compatible with vigilance. Substituting equations 13 and 14 into equation 12 gives

$$F = \frac{(1-v)aD}{1+aD((1-p)H_t+(1-v)pH_t)} \tag{15}$$

Which can be simplified to give

$$F = \frac{(1-v)aD}{1+(1-vp)aDH_t} \tag{16}$$